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BULLETIN
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Buried Viable Seeds in a Successional Series of Old Field and Forest Soils

HENRY J. OOSTING AND MARY E. HUMPHREYS

(WITH TWO FIGURES)

INTRODUCTION

That seeds may germinate after prolonged burial under natural conditions has long been known. Salter (1857) reported a remarkable flora that appeared on mud upturned in the deepening of Poole Harbor, England. Similar instances were discussed by Becquerel (1907) in his review of odd floras observed on soil from excavations such as canals, wells, and race tracks. Shull (1914) described an exposed pond-bed which produced abundant vegetation.

Undoubtedly these reports and other similar observations led to the experimental burial of seeds by Duvel (1902, 1905) and Beal (1905). Duvel believed he had demonstrated that viability increases with depth of burial although Goss (1924), after study of the data of the same experiment, maintained that depth of burial affected vitality of the seeds but little. In 1930, Darlington (1931) reported that the seeds of four species buried by Beal in 1879 were still viable, indicating that some seeds may remain viable for 50 years when buried under proper conditions. The history of our knowledge of life-span of seeds has been adequately reviewed by Crocker (1938).

During the past 25 years there have been several investigations of naturally buried seeds in relation to above-ground vegetation. Brenchley and Adam (1915) estimated the seed content of arable land, using natural germination in the field as an indication of the buried population. Later, taking soil samples from the field and observing germinations in the greenhouse, Brenchley (1918) found that the seed content of different soil levels varied with the past history of the land. Warington (1924) showed

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that the type of manure used on land affected its weed flora and hence its buried seed population. More recently Brenchley and Warington (1933) concluded that crop, soil type, and method of cultivation may influence the species and abundance of buried weed seeds.

Systematic studies of buried seeds in the forest floor have not been made since the report of Peter (1893), who found that the seeds of woody species occurred in soils of old forest while soils of new forest contained seeds of species common to cultivated land.

This suggested the present study of a series of sites whose past history is known, and which, vegetationally, bear a successional relationship to each other. By sampling soils from stands of a complete successional series (pioneers to climax) something should be learned of the length of time that naturally buried seeds may lie in the soil and remain viable. At the same time, there might be correlations between these buried seeds and the ages of the stands, and there might even be some clues to the mechanics of plant succession within the series.

Stands of all ages are readily available in the vicinity of Durham, N. C., for it is common practice to abandon fields when they cease to produce profitable crops. After abandonment, a weed population appears which shows a definite succession. The dominance of *Leptilon canadense* (L.) Britton denotes a field that has been lying fallow one year, while asters (*A. dumosus* L. and *A. ericoides* L.) and ragweed (*Ambrosia artemisiifolia* L.) indicate that the field has not been under cultivation for two years. At least three years without cultivation may be inferred from the dominance of *Andropogon* (chiefly *A. virginicus* L.) in an old field. When seed trees are available the fields are soon invaded by pines (*P. taeda* L. or *P. echinata* Mill.) which frequently become dominant within ten years. About a century later many of the pines will have been replaced by oaks and hickories, which indicate the ultimate climax forest.

Since this successional series invariably develops on old fields in this section, the seeds of the dominant species at least must be widely and evenly distributed. Some of these seeds probably do not germinate and they must lie buried in the forest floor. It seems plausible, therefore, that some seeds produced in one community would be present in the soil when subsequent communities occupy the site. By sampling the soil of representative communities of a successional series and subjecting these samples to uniform conditions favorable for germination, the resulting seedlings should be evidence of buried viable seeds.

METHODS

In the month of November, 1937, soil samples were obtained from twenty sites located in the Durham Division of the Duke Forest. Ten

ages, determined by the time since abandonment, were included in the series. Each age was represented by two sites. The ages are typical of old field succession in the Piedmont, ranging from a field cultivated in 1937 through pine dominance to an oak-hickory forest. One pine stand (*P. echinata*) in each age class had been studied by Billings (1938). All stands were on Granville sandy loam or closely related soil types and none showed evidence of cutting or other serious disturbance. The following ages were sampled:

Dominant	*Years abandoned*
1. Cultivated in 1937	0
2. *Leptilon*	1
3. *Aster-Ambrosia*	2
4. *Andropogon*	5
	Age of dominants[1]
5. Pine	15
6. Pine	33
7. Pine	58
8. Pine	85
9. Pine	112
10. Oak-hickory	200 plus

Within each site and within each duplicate site, two rectangular sampling areas were chosen, as similar in slope, exposure and cover as could be found.[2] Each sampling area was 10 by 20 feet (paced). The areas were cross-marked with a cord at 2-foot intervals and the sampling points determined from Tippett's (1927) Random Sampling numbers. The soil sampler used was the outer case of one devised by Coile (1936) for obtaining undisturbed soil samples. This is a steel cylinder 5.3 inches deep and 3.7 inches in diameter, with a volume of about 57 cubic inches. To insure the same depth and volume of soil for each sample, the coarse leafy litter, down to the fermentation layer, was removed from the sampling points on the forest floor. Precautions were taken to prevent contamination by seeds from sources other than the samples. Twenty samples were taken from each sampling area and dumped together upon an oilcloth. The pile was thoroughly mixed and then quartered. From a randomly selected quarter, a volume of soil equal to four sample portions (228 cubic

[1] The fields dominated by pine were probably abandoned from five to ten years longer than the ages indicated for the trees. It is doubtful if the hardwood sites were ever cultivated, for the stands were very uneven-aged with many trees over 200 years old.

[2] We acknowledge with thanks the assistance of Professor F. X. Schumacher of the Duke School of Forestry who gave invaluable advice on sampling methods and statistical treatment of the data.

inches) was taken as a composite sample. Since sampling areas were duplicated in each site and two sites were sampled for each age class, the latter were each represented by four composite samples. These were bagged and stored at a temperature just above freezing until all samples were obtained.

All the soils were removed from the cold room on December 3 and each composite sample was placed in a wooden flat on the earthen floor of the greenhouse. To insure that no samples consciously received undue attention, the flats were filled and placed in the greenhouse in the order that the mixture of bags was removed from storage. The soils were kept moist by watering regularly. Since the samples, when spread in the flats, were only about an inch deep, some tended to dry out very rapidly. A thin mulch of powdered, sterilized sphagnum reduced evaporation. Two similarly mulched flats of sterilized soil were placed with the samples as a check on contamination by wind-borne seeds.

The first seedlings were removed on February 3, 1938, and as often thereafter as individuals matured to an identifiable condition they were removed. Competition was kept at a minimum by removing all but a few of the individuals of any species which was particularly abundant. Those remaining were permitted to flower and thus served to check identifications based on purely vegetative characters.

Several species, germinating early in the experiment, tended to flower at remarkably early stages in their development. These plants had scarcely made any vegetative growth and had the appearance of dwarfed alpine or arctic species. The phenomenon was probably a photoperiodic response to the short days of the winter and spring months. Later it was found that growth and consequently identification were facilitated by occasionally sprinkling the flats with a dilute solution of a standard commercial fertilizer.

RESULTS

Between February 3 and October 2, 1938, the germinations which resulted in the flats yielded 5,989 plants. All these plants were considered to be the product of seeds present in the soils when they were obtained from the several sites, for no seedlings appeared in the check flats. Germinations had apparently ceased when the last plants were removed in October. The numbers and distribution of plants for the duplicate sites of each age class are given in table 1. Unidentified seedlings, which numbered 125, are not included. Most of these did not mature sufficiently to develop recognizable characters.

The data are such that to discuss them it seemed desirable to know whether, for certain species, the germinations occurred in sufficient numbers, or were so distributed, that they could not reasonably be ascribed

to chance. Accordingly the numbers of germinations for each of the 127 species were treated according to the method of analysis of variance of Fisher (Snedecor, 1937). When, in table 1 or in the discussion, a species is termed significant its germinations proved to have significant differences between age classes when subjected to the F test of Snedecor's table 10.2. Similarly it was determined which of the species within the wooded areas showed significant differences between pineland and hardwood. A further comparison was made within the areas that were not wooded. Here the germinations from the *Andropogon* sites were compared with the most recently abandoned fields. This division for comparison was chosen because the *Andropogon* field represents the best development of an herbaceous community before the dominance of upland fields by pine. Since forested areas represent something quite apart from land recently under cultivation, analyses were made to determine species significant in a comparison between the open and forested areas.

TABLE 1

List of Species and Numbers of Germinations in Soils from Duplicate Sites of Successive Age Classes

SPECIES APPEARING IN CULTIVATED FIELDS	AGES OF SITES										SIGNIFICANT FOR:			
	0	1	2	5	15	33	38	85	112	OH	Whole	Open vs. Forest	Early vs. Andropogon	Pine vs. Oak
Allium spp.	19	3	18	10	0	..	..	..	..	..	x	x	..	..
	5	4	33	14	1	..	..	..	..	..				
Alopecurus carolinianus Walt.	14	..	..	..	..	..	..	..	..	..	..	..	..	..
	0	..	..	..	..	..	..	..	..	..				
Andropogon spp.	1	1	0	26	3	..	2	1	1	7	x	x	x	x
	4	1	1	33	0	..	1	0	2	1				
Barbarea verna (Mill.) Asch.	2	..	2	..	..	..	..	..	..	..	..	x	..	..
	0	..	0	..	..	..	..	..	..	..				
Cerastium viscosum L.	0	1	1	1	..	0	..	..	..	..	..	..	x	..
	1	0	0	5	..	1	..	..	..	..				
Cerastium vulgatum L.	0	..	..	1	..	..	..	..	..	..	..	x	..	..
	5	..	..	2	..	..	..	..	..	..				
Cyperus compressus L.	84	39	0	22	2	0	..	..	..	..	..	x	x	..
	34	154	18	0	15	3	..	..	..	..				
Cyperus flavescens L.	88	45	0	9	40	0	..	0	1	..	..	x	..	..
	60	427	13	2	62	1	..	2	0	..				
Digitaria sanguinalis (L.) Scop.	92	189	20	61	..	..	..	0	..	..	x	x	x	..
	66	142	49	17	..	..	..	3	..	..				

TABLE 1—*Continued*

	AGES OF SITES										SIGNIFICANT FOR:			
	0	1	2	5	15	33	58	85	112	OH	Whole	Open vs. Forest	Early vs. Andropogon	Pine vs. Oak
Erigeron and Aster spp.	1	8	1	1	3	0	2	0	1	2	..	x	..	..
	0	30	0	3	0	1	1	4	6	0				
Evonymus americanus L.	0	1	..	..	..	..	..	..	..	..	x	x	x	..
	1	2	..	..	..	..	..	..	..	..				
Fimbristylis autumnalis (L.) R. & S.	9	..	..	1	..	..	..	..	..	..	x	x	x	..
	6	..	..	0	..	..	..	..	..	..				
Fimbristylis laxa Vahl.	24	..	0	..	0	..	..	..	..	..	..	x	..	..
	6	..	1	..	1	..	..	..	..	..				
Gnaphalium purpureum L.	5	2	0	3	29	1	8	3	4	6	..	..	..	..
	0	34	1	6	8	4	0	3	3	7				
Houstonia spp.	0	..	1	..	..	..	2	148	31	31	..	x	..	..
	5	..	1	..	..	..	1	0	15	0				
Holosteum umbellatum L.	1	..	..	..	..	..	..	..	..	..	..	..	..	..
	0	..	..	..	..	..	..	..	..	..				
Juncus effusus L.	3	0	..	..	..	..	..	..	..	..	x	x	x	..
	1	1	..	..	..	..	..	..	..	..				
Krigia virginica (L.) Willd.	11	..	..	2	..	0	0	..	..	..	x	x	x	..
	15	..	..	3	..	1	1	..	..	..				
Linaria canadensis (L.) Dumont	8	10	0	0	19	3	3	1	..	..	x	x	x	x
	1	21	3	6	4	2	2	0	..	..				
Leptilon canadense (L.) Britton	3	7	1	0	..	..	0	..	0	3	..	x	..	x
	0	23	0	1	..	..	1	..	4	8				
Mollugo verticillata L.	4	1	2	3	0	1	0	1	..	..	..	x	..	x
	5	4	0	2	1	7	2	1	..	..				
Myosotis virginica (L.) BSP.	0	..	..	..	..	..	..	..	..	0	..	x	..	..
	3	..	..	..	..	..	..	..	..	1				
Oenothera laciniata Hill	1	2	2	0	5	..	..	..	..	..	..	x	..	..
	1	1	1	4	1	..	..	..	..	..				
Oxalis corniculata L.	4	0	2	4	..	..	5	1	9	5	..	x	..	x
	0	1	1	1	..	..	0	3	0	4				
Oxalis florida Salisb.	2	..	..	..	0	1	..	0	5	3	x	x	..	..
	0	..	..	..	2	0	..	2	5	0				
Oxalis stricta L.	14	1	5	2	0	0	4	0	2	0	..	x	..	..
	1	8	3	4	6	5	7	2	0	4				
Physalis virginiana Mill.	2	..	..	..	..	..	..	..	..	1	..	x	..	x
	0	..	..	..	..	..	..	..	..	0				

TABLE 1—*Continued*

	AGES OF SITES										SIGNIFICANT FOR:			
	0	1	2	5	15	33	58	85	112	OH	Whole	Open vs. Forest	Early vs. Andropogon	Pine vs. Oak
Plantago virginica L.	9	..	20	19	4	..	..	..	1	..	..	x	x	..
	1	..	0	67	3	..	..	..	0	..				
Polygonum Persicaria L.	2	..	..	0	1	..	..	..	..	..	..	x	..	..
	0	..	..	1	0	..	..	..	..	..				
Polypremum procumbens L...	1	8	0	56	385	572	1	135	7	..	x	x	..	..
	3	1	13	1	27	221	6	58	3	..				
Sagina decumbens (Ell.)	9	12	8	11	6	1	..	..	..	..	x	x	..	..
T. & G.	30	1	11	20	3	0	..	..	..	..				
Scleranthus annuus L.	0	..	..	0	1	..	..	..	..	..	..	x	..	..
	4	..	..	1	0	..	..	..	..	..				
Specularia perfoliata (L.) ...	2	2	10	4	10	..	1	1	..	..	..	x	x	..
A. DC.	3	6	0	14	1	..	0	0	..	..				
Stenophyllus capillaris (L.)..	1	14	0	10	13	16	0	33	..	..	..	..	..	x
Britton	5	0	2	5	6	4	1	24	..	..				
Sisymbrium thalianum (L.)..	0	23	9	0	..	..	..	1	..	..	x	x	x	..
J. Gay	9	68	2	8	..	..	..	0	..	..				
Veronica peregrina L.	60	0	8	0	3	2	..	0	2	0	..	x	..	..
	3	30	0	27	5	1	..	1	0	1				
SPECIES ADDED BY THE ONE-YEAR FIELDS														
Chenopodium ambrosioides L. ..	..	0	..	..	..	..	..	..	..	..	..	x	..	..
	..	2	..	..	..	..	..	..	..	..				
Cyperus sabulosus Mart. & ..	..	2	..	..	..	..	..	..	..	..	..	x	..	..
Schrad.	..	0	..	..	..	..	..	..	..	..				
Dactyloctenium aegyptium ..	..	0	..	..	..	..	..	..	..	..	..	..	..	..
(L.) Richter	..	1	..	..	..	..	..	..	..	..				
Danthonia spicata (L.) Beauv. ..	..	0	..	..	..	..	..	..	2	..	..	..	..	..
	..	2	..	..	..	..	..	..	0	..				
Draba verna L.	..	6	..	..	..	..	..	..	..	..	..	x	..	..
	..	54	..	..	..	..	..	..	..	..				
Eleusine indica (L.) Gaertn..	..	1	..	..	..	..	..	..	..	..	..	..	..	..
	..	0	..	..	..	..	..	..	..	..				
Hieracium Gronovii L.	..	0	1	1	0	..	..	..	..	0	..	x	..	
	..	1	1	1	2	..	..	..	..	1				
Oenothera biennis L.	..	0	..	..	..	..	..	..	..	..	..	..	..	..
	..	1	..	..	..	..	..	..	..	..				

TABLE 1—*Continued*

	AGES OF SITES										SIGNIFICANT FOR:			
	0	1	2	5	15	33	58	85	112	OH	Whole	Open vs. Forest	Early vs. Andropogon	Pine vs. Oak
Oxalis violacea L.	..	3	..	..	..	..	..	..	..	1	..	..	..	x
	..	0	..	..	..	..	..	..	..	3				
Solidago spp.	..	19	87	0	0	1	..	..	1	1	x	x	x	..
	..	14	78	5	12	1	..	..	12	0				
Trifolium arvense L.	..	0	..	7	..	..	..	..	..	..	..	x	..	..
	..	25	..	0	..	..	..	..	..	..				
Trifolium incarnatum L.	..	0	..	..	..	..	..	..	..	..	..	x	..	..
	..	3	..	..	..	..	..	..	..	..				
Xanthium cylindraceum	..	0	..	..	..	..	..	..	..	..	..	..	..	..
Millsp. & Sherff	..	1	..	..	..	..	..	..	..	..				
SPECIES ADDED BY THE TWO-YEAR FIELDS														
Amaranthus hybridus L.	..	..	1	..	..	..	..	..	..	..	..	..	..	..
	..	..	0	..	..	..	..	..	..	..				
Ambrosia artemisiifolia L.	..	..	1	0	1	1	..	..	..	..	..	x	..	..
	..	..	0	1	0	0	..	..	..	..				
Anthemis Cotula L.	..	..	0	0	1	0	..	..	0	0	..	x	..	x
	..	..	1	1	0	1	..	..	3	3				
Ascyrum hypericoides L.	..	..	0	2	1	..	0	..	1	..	x	x	x	..
	..	..	2	5	0	..	2	..	2	..				
Carara didyma (L.) Britton	..	..	0	..	..	..	..	..	..	..	..	..	..	..
	..	..	1	..	..	..	..	..	..	..				
Cyperus globulosus Aubl.	..	..	0	0	..	9	0	..	0	0	..	x	..	..
	..	..	1	3	..	0	2	..	2	1				
Diodia teres Walt.	..	..	1	..	..	..	..	..	..	..	..	x	..	..
	..	..	1	..	..	..	..	..	..	..				
Geranium carolinianum L.	..	..	2	..	..	..	..	..	..	..	..	x	..	..
	..	..	0	..	..	..	..	..	..	..				
Helenium tenuifolium Nutt.	..	..	2	..	..	..	..	..	..	..	..	x	..	..
	..	..	0	..	..	..	..	..	..	..				
Hypericum gentianoides (L.)	..	..	0	7	6	1	1	3	..	1	x	x	x	x
BSP.	..	..	3	15	7	3	0	0	..	0				
Hypericum mutilum L.	..	..	0	..	..	..	..	..	..	..	..	..	..	..
	..	..	1	..	..	..	..	..	..	..				
Lespedeza striata (Thunb.)	..	..	8	86	..	..	..	..	..	..	x	x	x	..
H. & A.	..	..	1	29	..	..	..	..	..	..				

TABLE 1—*Continued*

	AGES OF SITES										SIGNIFICANT FOR:			
	0	1	2	5	15	33	58	85	112	OH	Whole	Open vs. Forest	Early vs. Andropogon	Pine vs. Oak
Plantago aristata Michx.	..	..	0	1	..	..	..	..	..	..	..	x	..	..
	..	..	1	0	..	..	..	..	..	..				
Plantago heterophylla Nutt.	..	..	0	..	..	..	..	..	..	..	..	x	..	..
	..	..	8	..	..	..	..	..	..	..				
Pyrrhopappus carolinianus (Walt.) DC.	..	..	0	..	..	..	..	..	..	..	..	..	..	..
	..	..	1	..	..	..	..	..	..	..				
Solanum carolinense L.	..	..	0	..	..	..	1	..	0	..	..	..	..	..
	..	..	1	..	..	..	0	..	1	..				
Specularia biflora (R. & P.) F. & M.	..	..	4	0	..	..	..	..	..	..	..	x	..	..
	..	..	0	1	..	..	..	..	..	..				
Veronica arvensis L.	..	..	3	0	..	..	..	1	..	..	..	x	x	..
	..	..	0	18	..	..	..	0	..	..				
SPECIES ADDED BY THE FIVE-YEAR FIELDS														
Agrostis hyemalis (Walt.) BSP.	..	..	..	0	..	..	..	..	0	..	..	x	x	..
	..	..	..	2	..	..	..	..	2	..				
Aristida spp.	..	..	..	6	0	..	..	..	..	..	..	x	x	..
	..	..	..	1	2	..	..	..	..	..				
Cassia nictitans L.	..	..	..	4	..	..	..	..	..	..	x	x	x	..
	..	..	..	13	..	..	..	..	..	..				
Eragrostis pilosa (L.) Beauv.	..	..	..	0	..	..	..	..	..	..	..	..	x	..
	..	..	..	1	..	..	..	..	..	..				
Euphorbia Preslii Guss.	..	..	..	0	..	..	..	..	..	..	..	..	x	..
	..	..	..	1	..	..	..	..	..	..				
Festuca octoflora Walt.	..	..	..	0	0	..	..	..	0	..	..	x	..	..
	..	..	..	2	1	..	..	..	7	..				
Festuca ovina L.	..	..	..	7	..	..	..	..	..	..	x	x	x	..
	..	..	..	2	..	..	..	..	..	..				
Poa annua L.	..	..	..	1	..	..	..	..	..	..	..	..	x	..
	..	..	..	0	..	..	..	..	..	..				
Poa cuspidata Nutt.	..	..	..	15	..	..	..	..	..	..	..	x	x	..
	..	..	..	0	..	..	..	..	..	..				
SPECIES ADDED BY THE FIFTEEN-YEAR SITES														
Cyperus inflexus Muhl.	..	..	..	..	0	..	..	..	..	..	..	x	..	..
	..	..	..	..	1	..	..	..	..	..				

TABLE 1—*Continued*

	AGES OF SITES										SIGNIFICANT FOR:			
	0	1	2	5	15	33	58	85	112	OH	Whole	Open vs. Forest	Early vs. Andropogon	Pine vs. Oak
Eragrostis spectabilis	..	..	..	..	3	0	..	1	..	0	..	x	..	..
(Pursh.) Steud.	..	..	..	..	0	*2*	..	0	..	1				
Erechtites hieracifolia (L.) ..	..	..	..	..	1	..	..	..	1	1	x	x	..	x
Raf.	..	..	..	..	0	..	..	..	0	*2*				
Pagesia acuminata (Walt.) ..	..	..	..	..	0	..	1	..	..	..	..	x	..	x
Pennell	..	..	..	..	1	..	0	..	..	..				
Silene antirrhina L.	..	..	..	..	3	..	..	..	..	..	..	x	..	..
	..	..	..	..	0	..	..	..	..	..				
SPECIES ADDED TO THE THIRTY-THREE-YEAR SITES														
Chrysopsis graminifolia	..	..	..	..	..	0	..	..	..	..	..	x	..	..
(Michx.) Nutt.	..	..	..	..	..	*2*	..	..	..	..				
Eupatorium capillifolium ...	..	..	..	..	..	0	..	..	..	..	..	x	..	..
(Lam.) Small	..	..	..	..	..	1	..	..	..	..				
Panicum dichotomum	..	..	..	..	..	*5*	..	..	*2*	..	x	x	..	x
	..	..	..	..	..	3	..	..	0	..				
Panicum sphaerocarpon Ell...	..	..	..	..	..	11	0	0	0	..	..	x	..	x
	..	..	..	..	..	3	1	1	3	..				
Panicum villosissimum Nash.	..	..	..	..	..	0	0	3	4	1	..	x	..	..
	..	..	..	..	..	*5*	*2*	0	*2*	0				
Paspalum setaceum Michx. ..	..	..	..	..	..	1	..	..	..	..	..	x	..	..
	..	..	..	..	..	0	..	..	..	..				
Potentilla pumila Poir	..	..	..	..	..	0	*2*	..	..	0	..	x	..	x
	..	..	..	..	..	1	0	..	..	3				
Trichostema dichotomum L...	..	..	..	..	..	0	..	..	..	..	..	x	..	..
	..	..	..	..	..	1	..	..	..	..				
Viola sp.	..	..	..	..	..	0	..	..	..	..	..	x	..	..
	..	..	..	..	..	1	..	..	..	..				
SPECIES ADDED BY THE FIFTY-EIGHT-YEAR SITES														
Broussonetia papyrifera (L.)	..	..	..	..	..	..	1	..	..	..	..	x	..	..
Vent.	..	..	..	..	..	..	0	..	..	..				
Chrysopsis mariana (L.) Nutt.	..	..	..	..	..	..	0	..	..	..	..	x	..	..
	..	..	..	..	..	..	1	..	..	..				
Cyperus strigosus L.	..	..	..	..	..	..	5	..	..	5	..	x	..	x
	..	..	..	..	..	..	0	..	..	0				

TABLE 1—*Continued*

	AGES OF SITES										SIGNIFICANT FOR:			
	0	1	2	5	15	33	58	85	112	OH	Whole	Open vs. Forest	Early vs. Andropogon	Pine vs. Oak
Gnaphalium obtusifolium L.	..	..	..	..	..	..	0	..	..	..	..	x	..	..
	..	..	..	..	..	..	1	..	..	..				
Panicum anceps Michx.	..	..	..	..	..	..	0	..	..	..	..	x	..	..
	..	..	..	..	..	..	1	..	..	..				
Panicum philadelphicum Bernh.	..	..	..	..	..	..	1	..	..	..	..	x	..	..
	..	..	..	..	..	..	0	..	..	..				
Panicum xalapense HBK.	..	..	..	..	..	..	1	0	..	0	..	x	..	x
	..	..	..	..	..	..	0	1	..	3				
Rubus sp.	..	..	..	..	..	..	1	..	..	3	..	x	..	x
	..	..	..	..	..	..	0	..	..	0				
Sisyrinchium gramineum Curtis	..	..	..	..	..	..	1	..	..	..	..	x	..	..
	..	..	..	..	..	..	0	..	..	..				
Verbascum Thapsus L.	..	..	..	..	..	..	2	..	..	..	..	x	..	..
	..	..	..	..	..	..	0	..	..	..				
SPECIES ADDED BY THE EIGHTY-FIVE-YEAR SITES														
Diodia virginiana L.	..	..	..	..	..	..	..	1	..	..	..	x	..	..
	..	..	..	..	..	..	..	0	..	..				
Hypoxis hirsuta (L.) Coville	..	..	..	..	..	..	..	0	7	..	..	..	..	..
	..	..	..	..	..	..	..	10	0	..				
Juncus scirpoides Lam.	..	..	..	..	..	..	..	14	..	..	..	x	..	..
	..	..	..	..	..	..	..	0	..	..				
Oxydendrum arboreum (L.) DC.	..	..	..	..	..	..	..	1	..	..	..	x	..	..
	..	..	..	..	..	..	..	0	..	..				
Panicum commutatum Schultes	..	..	..	..	..	..	..	1	..	..	..	x	..	..
	..	..	..	..	..	..	..	0	..	..				
Sambucus canadensis L.	..	..	..	..	..	..	..	0	..	..	..	x	..	..
	..	..	..	..	..	..	..	2	..	..				
Ulmus alata Michx.	..	..	..	..	..	..	..	0	..	..	..	x	..	..
	..	..	..	..	..	..	..	1	..	..				
SPECIES ADDED BY THE 112-YEAR SITES														
Agrostis alba L.	..	..	..	..	..	..	..	..	1	..	..	x	..	..
	..	..	..	..	..	..	..	..	0	..				
Cyperus cylindricus (Ell.) Britton	..	..	..	..	..	..	..	..	0	..	..	x	..	..
	..	..	..	..	..	..	..	..	1	..				

TABLE 1—*Concluded*

	AGES OF SITES										SIGNIFICANT FOR:			
	0	1	2	5	15	33	58	85	112	OH	Whole	Open vs. Forest	Early vs. Andropogon	Pine vs. Oak
Liquidambar styraciflua L....	..	..	..	..	..	..	..	..	1	..	..	x	..	..
	..	..	..	..	..	..	..	..	0	..				
Panicum lanuginosum Ell.	..	..	..	..	..	..	..	..	0	..	..	x	..	..
	..	..	..	..	..	..	..	..	1	..				
Prunella vulgaris L.	..	..	..	..	..	..	..	..	0	1	..	x	..	x
	..	..	..	..	..	..	..	..	1	0				
Rhus copallina L.	..	..	..	..	..	..	..	..	1	..	..	x	..	..
	..	..	..	..	..	..	..	..	0	..				
Scleria pauciflora Muhl.	..	..	..	..	..	..	..	..	0	..	..	x	..	..
	..	..	..	..	..	..	..	..	1	..				
Trifolium procumbens L.	..	..	..	..	..	..	..	..	0	..	..	x	..	..
	..	..	..	..	..	..	..	..	1	..				
SPECIES ADDED BY THE OAK-HICKORY SITES														
Cercis canadensis L.	..	..	..	..	..	..	..	..	..	1	..	x	..	x
	..	..	..	..	..	..	..	..	..	0				
Eupatorium hyssopifolium L.	..	..	..	..	..	..	..	..	..	0	..	x	..	x
	..	..	..	..	..	..	..	..	..	1				
Galium pilosum Ait.	..	..	..	..	..	..	..	..	..	1	..	x	..	x
	..	..	..	..	..	..	..	..	..	0				
Hedeoma pulegioides (L.) ...	..	..	..	..	..	..	..	..	..	0	..	x	..	x
Pers.	..	..	..	..	..	..	..	..	..	1				
Lactuca sp.	..	..	..	..	..	..	..	..	..	1	..	x	..	x
	..	..	..	..	..	..	..	..	..	0				
Morus rubra L.	..	..	..	..	..	..	..	..	..	0	..	x	..	x
	..	..	..	..	..	..	..	..	..	1				
Panicum Ashei Pearson	..	..	..	..	..	..	..	..	..	0	..	x	..	x
	..	..	..	..	..	..	..	..	..	2				
Panicum Boscii Poir.	..	..	..	..	..	..	..	..	..	1	x	x	..	x
	..	..	..	..	..	..	..	..	..	3				
Scutellaria sp.	..	..	..	..	..	..	..	..	..	1	..	x	..	x
	..	..	..	..	..	..	..	..	..	0				
Sonchus asper (L.) Hill	..	..	..	..	..	..	..	..	..	0	..	x	..	x
	..	..	..	..	..	..	..	..	..	1				
Vaccinium sp.	..	..	..	..	..	..	..	..	..	0	..	x	..	x
	..	..	..	..	..	..	..	..	..	1				
Viburnum affine Bush.	..	..	..	..	..	..	..	..	..	0	..	x	..	x
	..	..	..	..	..	..	..	..	..	1				

DISCUSSION

1. Origin of the germinating seeds

The majority of the germinations must have been derived from naturally buried seeds, for there was an average of 3.8 seedlings per square inch of natural surface sampled. Soils of fields abandoned one year yielded 1,463 germinations from samples with a field surface area totaling only slightly over one square foot (171.8 square inches) and a volume of about half a cubic foot. This, combined with the fact that over 90 per cent of the total germinations from each of the fields abandoned one, two, or five years were of species found growing in successionally younger fields, seems highly indicative of buried viable seeds.

It might be supposed that germinations in the forest soils resulted from seeds which were transported to the areas sampled, and that seeds from plants of an old-field community may effect an entrance into the interior of a pine stand. However, it seems improbable that many of the seeds could sift through the litter and fermentation zone, because of the thickness of these two layers after the stand is more than 20 years old. Billings (1938) charted the changes in the soil profile from an *Andropogon* field through the successional series of pine stands used in this investigation. The "plowed" horizon decreases, because it is becoming slowly incorporated in the A_2 horizon beneath it and the new A_1 horizon forming above it. The seeds buried in the plowed horizon are therefore incorporated in the A_1 and A_2 as the profile changes; they are not actually compacted in a layer of soil of decreasing width. Above the mineral soil there is a gradual accumulation of litter with the accompanying formation of the fermentation layer. The litter layer increases from nothing in an old field to well over one and a half inches in the mature pine stands. The fermentation zone gradually reaches a depth of over half an inch in the mature stands. It is conceivable that, if the seeds were retained in this zone, conditions would be favorable for their germination in the damp mycelial mat of the fermentation layer soon after their entrance into the stand. After germination, survival of the seedlings would depend upon their ability to compete with the new environmental condition. Any seeds germinating in the forest obviously could not be present to account for germinations in the flats. Those seeds of the old-field species which do germinate and survive in pine stands are limited in number (Billings) and decrease rapidly with each succeeding age class. Most of them probably do not reach the seed production stage before they die. Hence they are not responsible for the viable seeds in the forest floor.

The germinations of open-field species are undoubtedly products of seeds that were incorporated in the soil during cultivation or that entered

during the early years of abandonment. It is reasonable that these species would contribute most since their seeds have not had to penetrate a litter and fermentation layer in order to be mixed in the "plowed" horizon. Seeds of characteristic forest species could not have been produced in the old fields. Since they appeared only in the flats of forest soil, they must have the ability to effect an entrance into the soil and their seedlings must be so adapted that they survive where old-field species cannot.

It is doubtful that any germinations in the oak-hickory soils were produced by seeds which lay buried in the soil since their formation in some earlier successional community. All evidence indicates that the oak-hickory sites have never been cultivated. Studies now in progress indicate that several of these species, typical of the early stages in old-field succession, are practically eliminated as pine stands mature but that they may again be characteristically present in the mature hardwood forest. Their reappearance may be correlated with the opening of the stands as they become over-mature and possibly with the changed leaf litter.

2. Distribution of numbers of germinations

Table 1 gives the number of germinations for the species as distributed in the different age classes. Those species germinating in soils from the greatest number of age classes are, without exception, species which appear first (successionally) in the most recently abandoned field. Only *Gnaphalium purpureum* and *Polypremum procumbens* were represented in all age

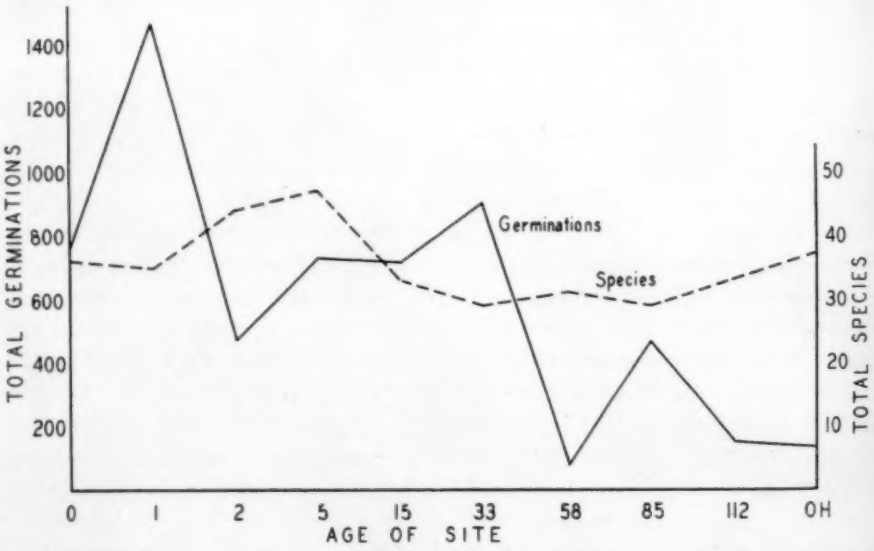

Fig. 1. Total germinations and total species that appeared in the soils from each age class.

classes. The species of recently abandoned fields not only appeared in the greatest number of age classes but also made up the largest percentage of total species in each age class except oak-hickory. Every age class had "new species," meaning species which did not appear in soils from any lesser-aged stand.

Figure 1, in which all germinations are graphed, shows that the greatest number of germinations occurred in the soils of the 1-year fields while the greatest number of species appeared in soils from the 5-year fields. However, all that can be said of the total seed population should properly apply to the 21 species significant for the whole experiment. Their germinations are graphed in figure 2. The two peaks of germinations are here reversed, with the 33-year stand having by far the greatest number. This high value is the result of the excessive number of germinations of *Polypremum procumbens*, a significant species but, in other age classes, of much less importance. Of the significant species, the greatest number was again in the 5-year soils.

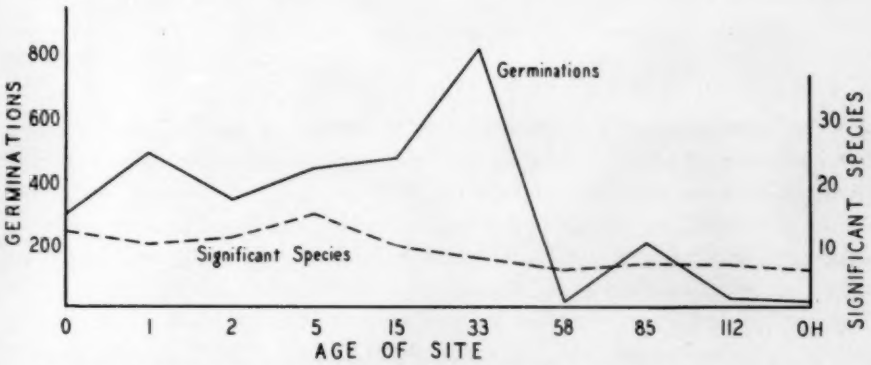

Fig. 2. Total significant species and their germinations for each age class.

Consideration of the distribution of significant species yields only a few generalizations. Those species producing sufficient germinations to be significant for the whole appeared first in open fields and younger pine stands. In spite of the numerous species and high germination counts for open fields, there were relatively few (25) species significant in the comparison between early fields and *Andropogon* dominance. Twelve of these species appeared in the cultivated field and eight did not come till *Andropogon* was dominant. The values serve to emphasize a correlation with the actual vegetation. Although many species are always present, only a few are dominant in size and numbers. The distinctness of the *Andropogon* field may be judged from its addition of nine species of which eight were significant in a comparison with earlier fields.

The comparison of open sites with wooded sites gives the most striking values for significant species. High percentages of the species added by each age of field were significant in this comparison, the cultivated field having 86 per cent. The consistent significance here is interpreted as an indication of the open-field nature of all these species. On the other hand, species appearing first in wooded stands were, without exception, all significant in the comparison. It cannot be entirely a matter of chance that those species which appear only in the soil from wooded stands should all then appear in significant numbers. Their seeds must not be transported elsewhere, or, as is more probable, must require the conditions of forest soil to retain viability.

The pine-hardwood comparison shows several early old-field species carrying over into pine stands in such numbers as to be significant. Those significant for pine were added in the young-to-middle-aged stands. The 85-year (mature) stand added no significant species and the over-mature (112-year) stand only one. Added species for the hardwood stand were, as before, all significant, these last added species being the portion of the viable seed population which is directly correlated with the dominants.

3. Relationships to Vegetation and Succession

The germinations of individual species become of special interest when considered in relation to their occurrence under natural conditions. All of the pine sites sampled in this study have been adequately described (Billings, 1938) on a phytosociological basis, and unpublished quadrat data (Oosting) are available for the oak-hickory stands and for herb stages of old-field succession. The general trend of old-field herbs begins with the abrupt appearance of large numbers of individuals which rarely maintain their importance for more than a year. The succeeding year finds the numbers materially reduced and thereafter there is a more or less gradual decline as trees become dominant. Many herbs of open old fields disappear entirely when trees appear, most are gone when the stand has attained middle age.

If the seeds of early old-field species are not especially viable, a natural break in the germination data should appear between the 5-year field and the 15-year pine. Also, if certain species germinate in soils from wooded stands in which, under natural conditions, Billings did not find them, these germinations should be excellent evidence of buried viable seeds, for the sampling is estimated at only 1 in 10,000.

The list of germinations includes 18 species of open-field herbs which appeared consistently for all age classes through 85 years or more. Of these species only three are recorded as growing naturally on the wooded sites and these only in the youngest stand. All are species which occur

consistently in old fields, usually with high frequencies and densities. Obviously they have been eliminated from membership in the forest community, although some are able to maintain themselves a few years longer than others. The general tendency for numbers of germinations to decrease with increased age class is apparent and is a strong argument for the existence of buried viable seeds, the viability decreasing with age. Reasoning on this basis, more evidence is available. Germinations of several open-field species are constantly present for all sites through the lesser age classes of pine. It might be concluded that seeds of these species had all germinated, or, what is more likely, that they were less viable and consequently died in the soil.

Certain inconsistencies in the distribution of numbers for individual species cannot be explained. *Polypremum procumbens* is a typical open-field herb and is not recorded as growing in pine forest, but it produced 412 seedlings in the 15-year age class and the remarkable number of 793 in the 33-year class. No other species approached these figures in total germinations. In contrast, the species of *Houstonia*, usually abundant in field and forest alike, produced no germinations in the 15- or 33-year soils although numerous in the soils from older stands.

In general, the counts for species that are statistically significant and are also listed in the quadrat records of the forested stands show no correlation with the above-ground vegetation. Of these species, only ten appear in the vegetation lists and many other species on the lists did not produce germinations in soil from any age class.

For herbaceous stands the numbers of germinations for an age class may sometimes be correlated with dominance in the previous age class and again may be an indication of what species will be important in the succeeding class. If, regardless of significance, the herb field species with highest germinations are considered by age classes, certain relationships to the field vegetation become apparent. The dominant weed species on a cultivated field at the end of the growing season is *Digitaria sanguinalis*. After a year of abandonment *Digitaria* is even more abundant and *Leptilon canadense* forms an open over-story three feet tall or more. A field abandoned two years is usually characterized by *Aster ericoides* or *Ambrosia artemisiifolia* or both. Thereafter a mixture of species is possible with *Andropogon* rapidly gaining dominance so that by the fourth year it is usually the most important species.

The species with high germinations are all regularly found in the old fields, although some have only seasonal importance. The species of *Sagina*, *Krigia*, *Sisymbrium*, and *Draba* are small in stature and abundant only vernally. Others appear only locally or are dwarfed by the larger and more conspicuous dominants.

The high germinations for *Digitaria* and the trend in numbers correlate well with the distribution under field conditions. It is surprising that the field just cultivated yielded no *Leptilon* seedlings for, under normal conditions, it would surely have supported a goodly number of individuals the next year if left fallow. The number of *Leptilon* germinations for the 1-year field is related to the number of plants growing there and indicates their probable presence in the field the next year. Actually, 2-year fields have numerous *Leptilon* plants but they are invariably dwarfed and depauperate. Indications are that by the third year most of the seeds will have germinated, and probably the dwarfed plants produce few seeds, so that *Leptilon* is soon eliminated from the old-field flora. The germination evidence supports these observations.

Germinations from 2-year fields are remarkably unrelated to aboveground observations. Normally *Aster ericoides* and *Ambrosia* are the dominants, as they were on the fields sampled. Peculiarly, not more than one germination of *Ambrosia* was recorded for any age class. Difficulties with identifications made it necessary to lump all germination counts of *Aster* and *Erigeron*, but the combined value may be used as indicative of *Aster* importance. Evidently the *Aster* germinations from the 1-year field are indicators of the *Aster* dominance to come in the next year. Although *Aster* was a dominant on the 2-year field only one germination occurred in the samples. There must have been many more seeds present. Since the samples were collected in the fall and, except for the brief storage in the cold room, thereafter never exposed to winter temperatures, it is possible that the seeds require an after-ripening period. This deficiency may also have contributed to the lack of germinations of *Ambrosia* (*A. trifida* L. requires after-ripening; Davis, 1929) and possibly other species as well.

The 5-year field had a good stand of *Andropogon virginicus*, characteristic for the age class. The clumps were uniformly distributed and spaced from about 6 inches to 2 feet apart. The appearance was that of a pure stand with complete dominance. However, between the clumps were numerous undersized plants of several species, almost all of which had been present on younger fields. The germination lists indicate that little or no *Andropogon* would have appeared on the 2-year field during its third year of abandonment. This conforms with field conditions, for the major appearance of *Andropogon* is apt to be in the fourth year. Germinations in the 5-year samples indicate a potential increase in the *Andropogon* population although actually it had probably about reached its maximum.

Many species present in abundance in the early fields produced no germinations in the wooded stands. This may be an indication that the

seeds of these species cannot retain their vitality for a long period of years. Evidence to support this idea is the fairly sharp decrease in the number of seeds germinating in soils from the 15-year pine as compared to the 5-year field. *Allium* drops from 24 to 5; *Digitaria* from 78 to 0; *Plantago virginica* from 86 to 7; *Cassia* from 17 to 0; *Lespedeza* from 115 to 0; and *Veronica peregrina* from 27 to 8. All of these species are statistically significant in the comparison between open and forested sites. To be sure, this radical decrease in germination may have been the result of germinations occurring naturally in the period between the field and the 15-year pine and not a loss of viability. These data are insufficient to prove either point.

Of the nine species added to the germination lists by the 5-year field seven were grasses. Numbers of germinations were not high and were rather in proportion to the importance of the species in this grass stage of old field succession. They represent an ephemeral condition which, with *Andropogon*, gradually disappears when trees become dominant. Billings (l. c.) found a few plants of *Andropogon* and *Eragrostis pilosa* in the 15-year pine stand, but *Andropogon*, *Aristida* and *Festuca octoflora* were the only species to produce germinations for this age class and they yielded only 3, 2 and 1, respectively.

Age classes beyond the establishment of pine show little correlation between natural vegetation and germinations. Numbers of herbs in pine forests are very small compared to those in open fields. With the relatively small soil samples used it is perhaps unwise to draw any conclusions. It is certain that, under natural conditions, field herbs decrease abruptly in total numbers and species with the development of pine. In a young stand of pine most of the old field herbs are eliminated and by middle age only scattered individuals remain, if any at all. At the same time new species of forest herbs have appeared, gradually increasing in abundance though never approaching open field numbers. The germination records show that viable seeds in the soil of these stands tend to include more and more species of wooded areas as the stands mature. However, the numbers never approach the concentrations of open fields.

When a forest stand becomes mature or over-mature, disturbances such as falling trees, etc., are not uncommon. If such a disturbance opens the crown cover and disturbs the accumulated litter there will immediately appear a crop of herbaceous species not at all related to the surrounding forest stand. These are the same species which, although characteristic of herb field succession, may appear sporadically in the forest quadrat records with very low densities and frequencies. They are likewise the same species which, producing tremendous numbers of germinations in open field soils, dropped off abruptly in soils where pine became dominant

but showed scattered germinations for age classes up to 112 years. Both the irregular appearances in undisturbed stands and the mass appearance in disturbed areas may reasonably be interpreted as resulting from buried viable seeds, for the presence of these seeds is here demonstrated by germination records.

It is disappointing to find no seedlings of the woody dominants in the soil from the forested sites. Sixteen species of woody seedlings were recorded with five of the species occurring in the oak-hickory site.

SUMMARY AND CONCLUSIONS

1. It is known that buried seeds may remain viable for long periods and studies have been made of naturally buried seeds as related to the vegetation.

2. To determine possible relations between buried seeds and past and future vegetation, soil samples were taken from a series of abandoned fields of known age and vegetative composition: a field under cultivation that season; fields fallow for 1, 2, and 5 years; shortleaf pine stands of 15, 33, 58, 85 and 112 years of age; and an oak-hickory forest. All stands had previously been studied phytosociologically and it is known that the series is representative of old field succession in the area.

3. Exposed to greenhouse conditions for 37 weeks the samples produced 5,989 seedlings. The seedlings represented 127 species of which 16 were woody ones.

4. The highest total germinations were produced by soil from the field which had been abandoned but one year. The 5-year field produced the greatest number of species.

5. The germination of seeds of several species in soil from habitats in which the parent plants do not grow indicates the possibility that, under natural conditions, seeds may lie buried for long periods and retain their viability.

6. Probably some seeds do not retain their viability under natural conditions, for several species which were very numerous in the stands of one age class produced few or no germinations in soil samples from the next succeeding class.

7. Statistical analyses of the occurrences of each of the species were made to ascertain which were significant throughout the series; in comparisons between open and forest; between the 5-year field and the preceding fields; and between pine and hardwood. The distribution of significant species serves to emphasize a relationship between vegetation and buried seeds; the distinctness of *Andropogon* fields; a difference between field and forest and between pine and hardwood; and that forest seeds apparently require forest conditions to retain their viability.

8. The germinations demonstrate the presence of viable seeds in the soil of all age classes sampled, but age and origin of the seeds remain problematical. They show a succession of species, as do the plants above ground, and, in general, they are indicative of that same succession.

DEPARTMENT OF BOTANY
DUKE UNIVERSITY
DURHAM, NORTH CAROLINA

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Additions to Florida Fungi—V[1]

WILLIAM A. MURRILL

The pileate species of the Hydnaceae are not abundant in central Florida nor are they exceptionally difficult, but the resupinate forms are many and intricate. Among the former, *H. zonatum*, *H. repandum*, *H. adustum*, *H. ochraceum*, *H. pulcherrimum*, and *H. erinaceus* are quite common; while *H. velutinum*, *H. diabolus*, *H. flavum*, and *H. rawakense* are frequent, and *H. fennicum*, *H. albidum*, *H. cristatum*, and *H. reniforme* either rare or very rare. Some of our most prominent and familiar northern species, such as *H. imbricatum*, *H. laciniatum*, *H. septentrionale*, *H. floriforme*, and *H. amicum*, are missing altogether; but resupinate species, like *H. plumosum*, *H. fasciculare*, and *H. fragilissimum*, more than fill their places.

Connecting links between this family and the Polyporaceae, such as *Irpiciporus lacteus*, *I. mollis*, and *Hydnochaete olivacea*, are commonly met with in the hammocks. Only one *Hydnum* (*H. floridanum* Berk. & Cooke) has previously been described from the Gainesville region and its description is rather too brief to be convincing.

Sarcodon alachuanum Murrill, sp. nov. Pileo convexo-subdepresso, 4–9 cm. lato, isabellino, disco fulvo, sapore farinaceo; sporis 4–5μ, stipite ferrugineo, 2–3 × 1–1.5 cm.

Pileus mostly circular, obconic to nearly plane or slightly depressed, gregarious or subcespitose, 4–9 cm. broad; surface smooth or somewhat uneven to colliculose, finely and densely short-pubescent, white to isabelline, fulvous on the disk with age, light-blue on the growing margin, which is rather thick, even, sterile, and usually somewhat lobed; context thick, mostly tough or woody, zonate, dark-blue when cut, with strongly farinaceous odor and farinaceous, nutty taste; teeth reaching 5 mm. long, dense, mostly terete, tapering, rusty-orange when young and fresh, fuliginous when dried; spores mostly globose, brownish, echinulate or tuberculate, about 4–5μ; stipe short, irregular, ferruginous-orange, hard or spongy, like the context within, about 2–3 × 1–1.5 cm.

Type collected by W. A. Murrill on the ground in woods at Gainesville, Fla., September 7, 1932 (*F 8335*). Also collected by the author at Gainesville, usually under oaks, from July to late September (*F 8402*, *F 18419*, *F 18423*, *F 18435*). Suggesting *H. ferrugipes* Coker and *H. cyaneotinctum* Peck but plaintly distinct from both.

Steccherinum subrawakense Murrill, sp. nov. Pileo conchato, 3–6 cm. lato, albo, glabro, sulcato; sporis ellipsoideis, hyalinis, 2.5–3 × 1–1.5μ.

[1] The numbers cited in this article refer to specimens permanently deposited in the herbarium of the Florida Agricultural Experiment Station, at Gainesville. One species from Virginia is included.

Pileus conchate, flabelliform to dimidiate, imbricate, 3–4 × 3–6 × 0.5–1 cm.; surface white, glabrous, sulcate, nodulose to colliculose; margin thin, sterile, even, entire to undulate or slightly lobed; context tough, white, odorless, 2–4 cm. thick, drying rigid and woody, white or isabelline; teeth firm and tough, white, unchanging, terete or flat, pointed, simple or divided at the tip, crowded, 2–10 mm. long, yellowish or grayish in dried specimens; spores ellipsoid, smooth, hyaline, 1-guttulate, about 2.5–3 × 1–1.5μ.

Type collected by E. West and W. A. Murrill on a hardwood log in South Planera Hammock, eleven miles northwest of Gainesville, Fla., October 26, 1938 (*F 18420*). Found only once. Easily distinguished from *S. Westii* Murrill and other relatives.

Steccherinum Westii Murrill, sp. nov. Pileo effuso-reflexo, imbricato, dimidiato, 2–6 cm. lato, zonato, subglabro, pallido ad cremeo; sporis subglobosis ad ellipsoideis, hyalinis, 2μ longis.

Pileus effused-reflexed, laterally connate, imbricate; reflexd portion dimidiate, convex to expanded, 1–2 × 2–6 × 0.2–0.4 cm; surface subglabrous, zonate, rosy-isabelline to cremeous; margin pruinose, white, entire or undulate, very thin, sterile, deflexed on drying; context membranous, white, unchanging, fragile when dry; teeth terete, small, sharp, crowded, white, unchanging, 2–3 mm. long, fragile, the tips concolorous; spores subglobose or broadly ellipsoid, smooth, hyaline, 1-guttulate, copious, about 2μ long.

Type collected by E. West and W. A. Murrill on an oak log at Newnan's Lake, Fla., July 30, 1938 (*F 18006*). Also collected by A. S. Rhoads on a hardwood log at Hawthorn, Fla., August 18, 1935 (*F 8421*). Resembling *S. rawakense*.

Hydnum virginianum Murrill, sp. nov. Pileo convexo-subdepresso, 8–12 cm. lato, glabro, castaneo, lobato, sapore grato; sporis globosis, praetuberculatis, hyalinis, 4–5.5μ; stipite 2–3 × 2.5 cm.

Pileus irregularly circular, thick, convex to somewhat depressed, gregarious, 8–12 cm. broad; surface glabrous, castaneous, margin incurved, undulate or lobed, thick, white; context thick, fleshy, with pleasant odor and sweet, nutty taste, white, unchanging; hymenium milk-white, brownish where bruised, wood-brown in dried specimens; teeth short, sharp, crowded; spores globose, hyaline under microscope, roughly tuberculate, about 4–5.5μ; stipe very short, white to concolorous or paler, about 2–3 × 2.5 cm.

Type collected by W. A. Murrill under pines at Lynchburg, Va., October 22, 1926 (*F 18608*). Although the author collected a large number of hydnums in the vicinity of Lynchburg, this one was found only once. He decided that it must be edible but, fortunately, resisted the temptation to make sure of it.

Scutiger subrubescens Murrill, sp. nov. Pileo convexo-plano, 6–9 cm. lato, subtestaceo, squamuloso, felleo; tubulis albis ad sulphureis vel rosaceis, parvulis; sporis ovoideis, 4–5 × 2.5–3μ; stipite 2–4 × 1–2 cm.

Pileus subcircular, thin, convex with umbo to plane or somewhat depressed, gregarious, 6–9 cm. broad; surface pale-testaceous at the center fading out to nearly white on the margin, dry, rather smooth, decorated with tufts of fibrillose squamules, erect, dark-colored and conspicuous on the disk but reduced to mere specks near the margin, which is even, straight, very thin, fertile, undulate to deeply lobed; context thin, fleshy-tough, rigid and friable when dry, white or faintly pinkish, soon becoming quite bitter, having the odor of burnt sugar after drying; hymenium even, decurrent, white to sulfur-colored, usually becoming bay when dried except at the margin, which becomes pink; tubes circular to slightly angular, very short, 4–5 to a mm., walls very thin, becoming lacerate; spores ovoid, smooth, hyaline, copious, 1-guttulate, 4–5 × 2.5–3μ; cystidia none; stipe subequal, uneven, central or eccentric, glabrous, often changing to reddish-brown when dried, 2–4 × 1–2 cm.

Type collected by E. West and W. A. Murrill on the ground under oaks at Gainesville, Fla., November 23, 1938 (*F 18411*). A very interesting species, related to *Polyporus fractipes*, *P. laeticolor*, *P. Whiteae*, and *P. confluens*. It grows in leaf-mold, unattached to roots or other buried wood. The hymenophores are neither cespitose nor multiplex, though often quite lobed and irregular. The tufts of fibrils are mostly erect, not imbricate, and give the disk a tomentose appearance when dried. The change in color is both surprising and confusing because it does not always happen, even in large specimens, but as a rule the mature tubes change when dried while the young ones remain white or become pink. The surface and flesh of the cap do not undergo this change but either retain their original color or fade slightly. As to the odor of burnt sugar, it developed only during the drying process in an electric oven but remained strong and distinct in the herbarium. Oxidation processes are complicated and may be left for the chemist to discuss.

Russula incarnaticeps Murrill, sp. nov. Pileo convexo-depresso, 6–9 cm. lato, incarnato, striato, sapore grato; lamellis adnatis, latis, sporis cremeis, 8–10 × 7–8μ; stipite albo, 5–6 × 1.5–2 cm.

Pileus convex to deeply depressed, solitary or gregarious, 6–9 cm. broad; surface slightly viscid, smooth, glabrous, incarnate, margin striate, peeling, entire; context thin, white, odorless, mild; lamellae adnate, broad, ventricose, overlapping, close, equal, many-forked at the base, entire, white to slightly yellowish; spores globose or subglobose, distinctly echinulate, granular, cremeous in mass, 8–10 × 7–8μ; sterile cells frequent, hyaline, inflated at the base and abruptly tapering; stipe subequal, smooth, glabrous, white, unchanging, 5–6 × 1.5–2 cm.

Type collected by E. West and W. A. Murrill under oaks in Sugarfoot Hammock, November 23, 1938 (*F 18429*). A fine-looking, large, cool-weather species with very little flesh, drying light and fragile. The sterile cells are shaped like ink-bottles containing short-handled pens.

Russula lividirosea Murrill, sp. nov. Pileo convexo-plano, 5 cm. lato, livido, glabro, sapore grato; lamellis adnatis, albis, sporis globosis, albis, 6–7μ; stipite roseo, 3–4 $\times$ 1–1.5 cm.

Pileus convex to plane, solitary, 5 cm. broad; surface smooth, glabrous, lividous, or partly lilacinous, margin entire, even or faintly striate with age; context white, unchanging, thin, odor agreeable, taste nutty and sweet; lamellae equal, many-forked at the base, adnate with a slight decurrent tooth, slightly ventricose but narrow, subcrowded, entire, white to stramineous; spores globose or subglobose, rarely broadly ellipsoid, spinulose, 1-guttulate, hyaline, 6–7μ long; cystidia abundant, lanceolate or fusiform, hyaline, 50–80 $\times$ 10–15μ; stipe tapering upward, smooth, glabrous, solid, roseous, white at the base, 3–4 $\times$ 1–1.5 cm.

Type collected by W. A. Murrill under an oak in Gainesville, Fla., November 25, 1938 (*F 18451*). Also collected by the author under an oak in Gainesville, January 13, 1938 (*F 15930*). At first sight suggesting one of the color-forms of *R. Mariae* Peck but not at all pruinose and, of course, quite different microscopically. It is a beautiful species even for *Russula*, with its livid cap and pink stem, and seems to be very rare, appearing only in winter. The cystidia are wondrous to behold, either when attached to the gills or when floating by the score among the spinulose spores.

Russula roseitincta Murrill, sp. nov. Pileo convexo-subdepresso, 6 cm. lato, glabro, sapore grato; lamellis adnatis, furcatis, sporis albis, 8–9 $\times$ 6–7μ; stipite albo ad subroseo, 5 $\times$ 1.2 cm.

Pileus convex to plane, slightly depressed at the center, solitary, 6 cm. broad; surface slightly viscid when moist, smooth, glabrous, rosy-avellaneous-isabelline, margin even, entire, peeling; context thin, white, odorless, mild; lamellae adnate, equal, medium broad, rather close, many-forked at the base, a few midway, entire, white, unchanging; spores white, mostly broadly ellipsoid, 1-guttulate, conspicuously and densely echinulate, 8–9 $\times$ 6–7μ; sterile cells few, hyaline, inflated, 20–30 $\times$ 15μ, with threadlike tips of varying lengths; stipe equal, smooth, glabrous, white, rose-tinted when dry, 5 $\times$ 1.2 cm.

Type collected by E. West and W. A. Murrill on the ground in mixed woods at Newnan's Lake, Fla., November 15, 1938 (*F 18453*). Near *R. rosei-isabellina* Murrill but with different microscopic characters and gill structure.

Russula subacris Murrill, sp. nov. Pileo convexo-subdepresso, 3–5 cm. lato, glabro, rubro, acrido; lamellis adnexis, confertis, albis; sporis ellipsoideis, echinulatis, albis, 10 × 7μ; stipite glabro, albo, 1.5–3 × 0.5–1.3 cm.

Pileus convex to slightly depressed, gregarious, 3–5 cm. broad; surface smooth, glabrous, slightly viscid, varying from dark-incarnate to pale-purple; margin entire, even, often becoming quite striate with age, peeling very readily; context thin, white, unchanging, odorless, only moderately acrid; lamellae adnexed, slightly sinuate, equal, close, narrow, entire, pure-white, unchanging; spores chalk-white in mass, broadly ellipsoid, distinctly but not strongly echinulate, about 10 × 7μ; cystidia few, flask-shaped, hyaline, about 35 × 10μ; stipe equal or subequal, smooth, glabrous, milk-white, 1.5–3 × 0.5–1.3 cm.

Type collected by West, Arnold and Murrill in moist ground under deciduous trees at Planera Hammock, eleven miles northwest of Gainesville, Fla., January 3, 1939 (*F 19508*). Also collected by Mr. J. R. Watson in low grassy ground at Myakka Lake, Sarasota Co., Fla., December 26, 1938 (*F 19227*). A small red species which peels very readily but is not nearly so acrid as *R. emetica*. It appears only in midwinter.

Russula subgranulosa Murrill, sp. nov. Pileo convexo-depresso, 8 cm. lato, avellaneo, sapore grato; lamellis subadnexis, non furcatis, sporis stramineis, ellipsoideis, 9–10 × 6–7μ; stipite albo, 5 × 1.5 cm.

Pileus convex to depressed, solitary, 8 cm. broad; surface dry, avellaneous with yellowish tints, lilac at the center, the cuticle breaking into small granules visible under a handlens, margin even, entire, not peeling; context thin, white, unchanging, odorless, mild; lamellae just touching the stipe by a tooth, rounded behind, medium broad and medium distant, slightly ventricose, equal, none forked anywhere, entire, white to pale-yellow; spores mostly broadly ellipsoid, 1-guttulate, conspicuously echinulate, stramineous in mass, about 9–10 × 6–7μ; cystidia none; stipe equal, smooth, glabrous, slightly granular at the apex, white, with a rosy tint in one place, 5 × 1.5 cm.

Type collected by E. West and W. A. Murrill on the ground in mixed woods at Newnan's Lake, Fla., November 15, 1938 (*F 18433*). Near *R. roseitincta* Murrill but the spores are pale-yellow and the gills are not forked anywhere, even at the very base.

Melanoleuca margarita Murrill, sp. nov. Pileo convexo, 1.5–2 cm. lato, albo, subfelleo; lamellis albis, sporis ovoideis, 3–4 × 1.5–2μ; stipite albo, subradicato, subclavato, 4–6 × 0.4–0.8 cm.

Pileus convex, not expanding, gregarious, 1.5–2 cm. broad; surface smooth, dry, finely fibrillose, pearly-white with a bluish tint, margin even, entire to undulate; context white, odorless, not acrid but becoming slightly bitter; lamellae sinuate, plane, close, medium broad, inserted, entire, white, unchanging; spores ovoid, smooth, hyaline, 1-guttulate, 3–4 × 1.5–2μ; cystidia none;

stipe above ground subequal, smooth, slightly fibrillose, solid, white, mostly fulvous when dried, 2–3 × 0.4–0.6 cm.; buried portion clavate, not definitely radicate, 2–3 × 0.8 cm.

Type collected by E. West and W. A. Murrill on low ground under hardwood trees near Hogtown Creek, Gainesville, Fla., November 23, 1938 (*F 18454*). Suggesting *M. acris* (Peck) Murrill but not acrid and having smaller, ovoid spores.

Galerula Westii Murrill, sp. nov. Pileo conico-subexpanso, umbonato, gregario, 1–1.5 cm. lato, fulvo ad isabellino; lamellis adnatis, latis, sporis ellipsoideis, 8 × 5μ; stipite albo, 3–4 × 0.2–0.3 cm.

Pileus conic to subexpanded, umbonate, closely gregarious, 1–1.5 cm. broad; surface hygrophanous, fulvous when moist, isabelline when dry, becoming fulvous again after artificial drying, smooth, pruinose, margin even, straight and appressed when young; context very thin, white, odorless, mild; lamellae adnate, broad, distant, inserted, entire, pallid to subferruginous; spores ellipsoid, smooth, 1-guttulate, pale-ferruginous, about 8 × 5μ; cystidia none; stipe cartilaginous, equal, smooth, glabrous, white, 3–4 × 0.2–0.3 cm.; veil slight, whitish, disappearing at a very early stage and leaving no annulus.

Type collected by E. West and W. A. Murrill in damp soil under hardwood trees in Sugarfoot Hammock, near Gainesville, Fla., November 23, 1938 (*F 18428*). Abundant in the type locality but not found elsewhere. The conic umbo is prominent and rather distinctive.

Naucoria cuspidata Murrill, sp. nov. Pileo campanulato-depresso, umbonato, 1.5–3 cm. lato, fulvo; lamellis emarginatis, sporis ellipsoideis, tuberculatis, 8–9 × 5μ; stipite isabellino, 4–5 × 0.3–0.4 cm.

Pileus campanulate to depressed with a small conic umbo, gregarious, 1.5–3 cm. broad; surface hygrophanous, smooth, finely innate-fibrillose, uniformly fulvous, margin even, entire to undulate; context very thin, without characteristic odor; lamellae emarginate, medium distant, plane but rather broad, inserted, very thin, fringed on the edges, becoming ferruginous or fulvous; spores ellipsoid, obliquely apiculate, granular, finely but distinctly tuberculate, ferruginous, about 8–9 × 5μ; cystidia none; stipe fleshy with a tough rind, subequal, striate, fibrillose, isabelline, 4–5 × 0.3–0.4 cm.

Type collected by E. West and W. A. Murrill on damp ground under hardwood trees in Sugarfoot Hammock, near Gainesville, Fla., November 23, 1938 (*F 18432*). Suggesting *N. praeu nbonata* Murrill but differently colored and having tuberculate spores.

Gymnopilus armillatus Murrill, sp. nov. Pileo convexo-expanso, caespitoso, 5–10 cm. lato, glabro, ochroleuco, disco subluteo, praefelleo; lamellis sinuatis, confertis, sporis ellipsoideis vel ovoideis, 8–10 × 5–6μ; stipite striato, 10 × 1–1.5 cm., annulo amplo, persistente.

Pileus convex to expanded, cespitose, 5–10 cm. broad; surface smooth, not viscid, subglabrous to glabrous, ochroleucous, pale-luteous on the disk, margin even, entire; context thick at the center, pale-yellow, very bitter, odorless; lamellae broad, crowded, entire, sinuate with decurrent tooth, luteous-flavous, becoming fulvous with age; spores ovoid or ellipsoid, smooth, ferruginous 1-guttulate, 8–10 × 5–6μ; cystidia none; stipe equal, fleshy-tough, striate, fibrillose, pale-yellow at the apex, darker below, brownish or blackish at the base, about 10 × 1–1.5 cm.; annulus superior, ample, membranous, yellow, persistent.

Type collected by A. S. Rhoads on the root of a living sweet-gum tree, causing a whitish rot, at Bithlo, Orange Co., Fla., December 21, 1932 (*F 15731*). Cotype collected by J. R. Watson near oaks at Myakka Lake, Sarasota Co., Fla., December 26, 1938 (*F 19507*). A large, clustered species with a distinct ring; apparently confined to central Florida.

NEW COMBINATIONS

For the convenience of those who use Saccardo's nomenclature the following new combinations are made:

Galerula Westii = **Galera Westii**
Gymnopilus armillatus = **Flammula armillata**
Melanoleuca margarita = **Tricholoma margarita**
Sarcodon alachuanum = **Hydnum alachuanum**
Steccherinum subrawakense = **Hydnum subrawakense**
Steccherinum Westii = **Hydnum Westii**

HERBARIUM, FLORIDA AGRICULTURAL EXPERIMENT STATION
GAINESVILLE, FLORIDA

A Collection of Flowering Plants from Mount Roraima and adjacent Venezuela, British Guiana, and Brazil

By A. C. Smith (and collaborators)

Between September, 1938, and February, 1939, Mr. Albert S. Pinkus made a trip from Georgetown to the vicinity of Mount Roraima, during which he assembled 290 numbers of herbarium specimens in several sets. This collection comes from a region of extreme botanical interest, which has been visited by several collectors, but which, upon being revisited, always discloses new or otherwise noteworthy species. Mr. Pinkus' route took him up the Mazaruni River in British Guiana to the Kurupung River, thence overland to the junction of the Mazaruni with the Kamarang River, which was ascended. Following the Pakaraima Mountains on the Venezuelan side, the collector reached Arabupu, the historic locality near the base of Mount Roraima. Three months were spent in this region, including ten days on the summit of Mount Roraima, which was ascended by means of the famous "Ledge." The return trip was made along the Pakaraima Range east of Mount Roraima to the head of the Kukui River, which was followed back to the Mazaruni region.

The few collections already made in the vicinity of Mount Roraima serve to emphasize the remarkable endemism of the flora. Perhaps the most interesting feature of Mr. Pinkus' work is the re-collection of some of the endemic species, many of which are represented by scanty material and which are better understood with every new visit to the region. Following is a list of species which were collected from essentially the type locality (summit or southwestern slopes of Mount Roraima, including the vicinity of Arabupu). Mr. Pinkus' collection number is indicated in italics following the name; in some cases the specimen represents the second collection of the species.

Nietneria corymbosa Kl. & Rich. Schomb., *107.*
Tofieldia Schomburgkiana Oliver, *290.*
Epidendrum alsum Ridley, *103.*
Epidendrum montigenum Ridley, *99.*
Octomeria Connellii Rolfe, *101.*
Pogonia parviflora (Lindl.) Reichb. f., *156.*
Sobralia stenophylla Lindl., *54.*
Roupala Schomburgkii Kl., *50.*
Ocotea roraimae Mez, *145.*
Weinmannia guyanensis Kl., *289.*
Weinmannia laxiramea Killip & Smith, *106.*
Licania rufescens Kl., *62.*
Ravenia ruellioides Oliver, *141.*
Qualea Schomburgkiana Warm., *64.*
Chaetocarpus stipularis Gleason, *56, 81.*
Cyrilla brevifolia N. E. Brown, *100, 155.*
Ilex retusa Kl., *120.*
Ouratea Tatei Gleason, *80.*
Poecilandra retusa Tul., *158.*
Sauvagesia Imthurniana (Oliver) Dwyer, *116.*
Archytaea multiflora Benth., *48.*
Bonnetia roraimae Oliver, *111.*
Myrtus roraimensis N. E. Brown, *102.*
Miconia rupestris Ule, *137.*
Miconia superba Ule, *66.*
Sciodaphyllum umbellatum N. E. Brown, *153.*

Befaria Tatei Gleason, *108.*
Ledothamnus sessiliflorus N. E. Brown, *104.*
Pernettya marginata N. E. Brown, *113, 114.*
Thibaudia formosa Kl., *128.*
Thibaudia nutans Kl., *39.*
Thibaudia Ulei (Mansf.) A. C. Smith, *105, 149.*
Bonyunia superba Rich. Schomb., *270.*
Calolisianthus Imthurnianus (Oliver) Gleason, *117.*
Symbolanthus Elisabethae (Schomb.) Gilg., *160.*
Cordia hirta Johnston, *69.*
Hyptis arborea Benth., *43.*
Orchyllium Campbellianum (Oliver) Gleason, *133.*
Orchyllium Humboldtii (Schomb.) Barnh., *151.*
Orchyllium Quelchii (N. E. Brown) Gleason, *118.*
Palicourea obtusata Krause, *126.*
Psychotria crassa Benth., *119.*
Psychotria oblita Wernh., *121, 148.*
Viburnum roraimense Killip & Smith, *138, 139.*
Baccharis Schomburgkii Baker, *125.*
Baccharis Vitis-idaea Oliver, *110.*
Calea Oliverii Robins. & Greenm., *76, 124.*
Eupatorium roupalifolium Robins., *159.*
Mikania pannosa Baker, *57.*
Quelchia conferta N. E. Brown, 112.
Stenopadus condensatus (Baker) Blake, *157.*
Vernonia ehretifolia Benth., *123.*

In the remainder of this treatment several noteworthy species are discussed, fifteen which are apparently new are described, and two new combinations are made. In identifying the collection I have enjoyed the kind collaboration of several specialists, and I take this opportunity to express appreciation to Messrs. S. F. Blake, L. Croizat, J. D. Dwyer, H. A. Gleason, E. P. Killip, H. N. Moldenke, P. C. Standley, L. O. Williams, and R. E. Woodson. Some of these have kindly permitted their work to be included in the present paper. The first set of the collection, including types unless otherwise noted, is deposited in the herbarium of the New York Botanical Garden.

SMILACACEAE

Smilax immersa A. C. Smith, sp. nov. Frutex scandens ubique praeter perianthii segmentos apicem versus minute et obscure tomentellos glaber; ramulis teretibus minute tuberculatis inermis; petiolis crassis 2.5–3.5 cm. longis, marginibus inflexis 7–10 mm. longis extremitate obtusis vel subacutis vaginatis, apicem versus incrassatis et rugosis; laminis coriaceis opacis ellipticooblongis, 10–19 cm. longis, 3.5–8 cm. latis, basi acutis vel attenuatis et in petiolum decurrentibus, apice breviter calloso-cuspidatis, margine anguste recurvatis, e basi 3-(vel obscure 5-) nerviis, nervis extimis inconspicuis, alteris supra valde impressis vel interdum planis subtus prominentibus, rete venularum subimmerso vel leviter prominulo; pedunculis umbellarum masculorum in racemis bracteatis ad 6 cm. longis dispositis vel raro solitariis; bracteis oblongis acutis 2–5 mm. longis; pedunculis 4–13 mm. longis paullo compressis; receptaculis masculis subglobosis circiter 2 mm. diametro, bracteolis oblongolanceolatis 0.5–1 mm. longis; floribus 15–30 per umbellam; pedicellis gracilibus 5–6 mm. longis; perianthii segmentis elliptico-lanceolatis, 3.5–4.5 mm.

longis, 1–1.2 mm. latis, acutis; filamentis membranaceis 1.5–2.2 mm. longis, antheris oblongis subacutis quam filamentis paullo brevioribus.

Type, *Pinkus 37*, collected October 3, 1938, along Membaru Creek, upper Mazaruni River region, British Guiana. *S. immersa* is characterized by its thick smooth elliptic leaf-blades with basal principal nerves and immersed veinlets, its unarmed stems, its inflorescences with several umbels, and its very slender pedicels. Its relationship appears to be with *S. Schomburgkiana* Kunth and *S. pseudosyphilitica* Kunth, species readily distinguished by their reticulate venation.

ORCHIDACEAE[1]

POGONIA PARVIFLORA (Lindl.) Reichb.f. Venezuela: southwestern slopes of Mount Roraima, alt. about 7200 ft., *Pinkus 156;* growing in swampy open places; perianth purple; stem and some leaves red. This collection, from the type locality, is of especial interest because the flowers are somewhat smaller than those previously known. Following is a description of the flowers based on *Pinkus 156:*

Sepals about 25 mm. long and 8 mm. broad, oblong-elliptic, acute, apiculate, about 7-nerved, navicular; petals about 22 mm. long and 10 mm. broad, oblong-obovate, obtuse or acutish, minutely denticulate, with about 7 principal nerves; lip about 22 mm. long and 13 mm. broad, obovate, entire or with a very small terminal lobe, the lamina with a fleshy bilamellate callus extending from the base to the apex, with two clavellate callous processes about 3 mm. long at the base of the lip, one on either side of the central callus; column about 18 mm. long, slightly arcuate; pollen simple, not in tetrads.

ROSACEAE[2]

Licania exiguifolia Standley, sp. nov. Arbor 10-metralis, trunco 15 cm. diam., ut videtur dense ramosa, ramulis gracilibus sed rigidis teretibus griseo-fuscis vel fusco-ferrugineis elevato-lenticellatis adpresso-pilosis vel strigosis, internodiis brevibus vel brevissimis; folia parva petiolata rigide coriacea, petiolo crassiusculo 4–5 mm. longo strigoso vel glabro; lamina oblongo-elliptica vel oblongo-ovata 3–5 cm. longa 1.5–2 cm. lata sensim vel subabrupte acuminata vel longe acuminata, basi acuta, supra in sicco fuscescens sub lucida glabra vel tantum ad costam valde impressam strigosa, nervis vix manifestis planis, subtus pallidior griseo-ochracea ubique densissime adpresso-tomentosa, ad costam nervosque adpresso-pilosa, costa crassiuscula elevata, nervis lateralibus utroque latere 7–8 prominentibus valde obliquis angulo semirecto adscendentibus marginem attingentibus, venis tomento fere omnino occultis; inflorescentia non visa; fructus depresso-globosus 2–2.5 cm. latus 1.7–2 cm.

[1] By L. O. Williams.
[2] By P. C. Standley.

altus, basi et apice latissime rotundatus lucidus brunneo-ferrugineus ubique dense pallido-lenticellatus.

Type, *Pinkus 245*, collected February 21, 1939, along trail between Membaru Creek and Makreba Falls on Kurupung River, upper Mazaruni region, British Guiana, and deposited in the herbarium of the Field Museum (dupl. in Herb. N. Y. Bot. Gard., etc.).

Licania roraimensis Standley, sp. nov. Arbor 18-metralis, trunco 30 cm. diam., ramulis teretibus in sicco griseo-fuscis rimosis elevato-lenticellatis, internodiis brevibus, novellis non visis; folia mediocria breviter petiolata rigide coriacea, petiolo crasso 7–10 mm. longo supra late canaliculato glabro vel glabrato; lamina elliptica vel oblongo-elliptica 9.5–13 cm. longa 4.5–6 cm. lata sensim vel subito attenuato-acuminata, acumine angusto longe attenuato usque 2 cm. longo, basi plus minusve obliqua obtusa vel anguste rotundata, supra sublucida glabra, costa plana, nervis venisque non elevatis subtus pallidior ochracea, glabrata sed inter venulas adpresso-tomentulosa, costa crassiuscula elevata, nervis lateralibus utroque latere 5–6 obliquis angulo semirecto vel paullo latiore adscendentibus subarcuatis marginem fere attingentibus, venulis prominentibus atque incrassatis arctissime reticulatis, margine quoque valde incrassato atque cartilagineo; inflorescentia (cum floribus imperfectis et vetustis tantum visa) terminalis vel axillaris racemoso-paniculata sessilis 6–10 cm. longa pauciramosa, ramis crassiusculis dense et minute sordido-puberulis, floribus sessilibus vel breviter crasse pedicellatis; calyx 4 mm. longus dense et minute puberulo-tomentellus campanulatus, lobis erectis ovato-ovalibus obtusis vix 1.2 mm. longis; cetera ignota.

Type, *Pinkus 61*, collected December 15, 1938, in the vicinity of Arabupu, Mount Roraima District, alt. about 4200 ft., Venezuela, and deposited in the herbarium of the Field Museum (dupl. in Herb. N. Y. Bot. Gard., etc.).

Licania pallidula Standley, sp. nov. Arbor 24-metralis, trunco 30 cm. diam., ramulis gracilibus teretibus ferrugineo-ochraceis rimosis elevato-lenticellatis, novellis ferrugineis glabris; folia mediocria brevissime petiolata coriacea rigida, petiolo crasso 3–5 mm. longo glabro; lamina elliptica, obovato-elliptica vel oblongo-obovata 7–9 cm. longa 3.5–5.5 cm. lata obtusa vel rarius anguste rotundata, basi acuta et subcontracta, supra plus minusve lucida in sicco pallide viridis glabra, costa prominente, nervis manifestis atque interdum prominulis, subtus glauco-viridis ubique costa nervisque exceptis tomento minutissimo pallido adpresso obtecta, costa prominente, nervis lateralibus utroque latere ca. 8 prominentibus tenerrimis angulo latiusculo adscendentibus remote a margine arcuato-conjunctis subarcuatis, venulis prominulis laxe reticulatis gracilibus; paniculae terminales atque axillares pauciramosae longe pedunculatae ca. 5 cm. longae, ramis rigidis adscendentibus ferrugineis sparse vel dense et minute

strigillosis, floribus (perfectis non visis) racemosis sessilibus vel brevissime et crasse pedicellatis; calyx persistens ca. 3 mm. longus dense minutissime ochraceo-tomentellus, dentibus rotundato-ovatis obtusis brevissimis erectis; fructus valde immaturus obovatus 7 mm. longus apice late rotundatus, basin versus sensim attenuatus, dense atque minutissime ochraceo-tomentellus.

Type, *Pinkus 89*, collected December 28, 1938, in second growth on clay soil, on southwestern slopes of Mount Roraima, vinicity of Arabupu, alt. about 4600 ft., Venezuela, and deposited in the herbarium of the Field Museum (dupl. in Herb. N. Y. Bot. Gard., etc.). An apparently well marked species, notable for the very minute tomentum that gives a glaucous appearance to the lower leaf-surface. In this, as in the other species here described, the specimens are in fruit or very advanced anthesis, so that it is impossible to describe the floral details.

CAESALPINIACEAE

DIMORPHANDRA CONGESTIFLORA Sprague & Sandwith. British Guiana: near Makreba Falls, Kurupung River, upper Mazaruni region, *Pinkus 7*. Excellent flowering material of a rare species, from the type locality.

DIMORPHANDRA CUPREA Sprague & Sandwith. British Guiana: Arubaru River (Kako tributary), upper Mazaruni drainage, near Mount Haiamatipu, alt. about 2000 ft., *Pinkus 203*. Previously known from the vicinity of Kaieteur Savanna.

DICYMBE JENMANI Sandwith. British Guiana: Membaru Creek, upper Mazaruni region, *Pinkus 31, 237*. Our material, compared with that previously known from Kaieteur Savanna, has the leaflets in two or three, rather than four, pairs, the veinlet reticulation somewhat more obvious on the upper leaf-surface, and the sepals uniformly sericeous without rather than sericeous only along a mid-line, but hardly appears to differ conspicuously. The collector notes the present specimens as trees 20 and 70 feet high. In the two flowers dissected there were 9 ovules in each ovary, 10 being mentioned in the original description.

FABACEAE

ALEXA IMPERATRICIS (Schomb.) Baker. British Guiana: upper Arubaru River (Kako tributary), Mazaruni drainage, alt. about 2000 ft., *Pinkus 171*. The collector reports that the bark of this tree, which is uncommon in collections, is used as a fish poison.

MALPIGHIACEAE

BLEPHARANDRA HYPOLEUCA (Benth.) Griseb. British Guiana: Membaru Creek, upper Mazaruni region, *Pinkus 28, 211*. This monotypic genus

appears to have been previously known only from the vicinity of Mount Roraima.

VOCHYSIACEAE

Vochysia Pinkusii A. C. Smith, sp. nov. Arbor ad 20 m. alta, trunco ad 30 cm. diametro; ramulis juventute quadrangulatis ferrugineo-subadpresso-hirsutis demum glabrescentibus; foliis oppositis, petiolis 10–15 mm. longis mox glabris, laminis coriaceis siccitate supra olivaceis oblongo-ellipticis, 10–14 cm. longis, 5.5–7.5 cm. latis, basi subacutis vel obtusis et in petiolum decurrentibus, apice cuspidatis vel breviter acuminatis (acumine 4–8 mm. longo obtuso), margine integris et leviter recurvatis, supra glabris, subtus brevissime et densissime ferrugineo-tomentellis demum glabrescentibus, costa ad apicem valida supra conspicue impressa subtus prominente, nervis secundariis utroque 15–20 patentibus curvatis prope (1–2 mm.) marginem conspicue anastomosantibus supra impressis subtus prominentibus, venulis inconspicuis; inflorescentiis terminalibus 1–3 racemiformibus 15–20 cm. longis; rhachide crassa ut ramulis hirsuta, pedunculis brevibus (ad 5 mm. longis) vel nullis, floribus binis vel solitariis; pedicellis gracilibus 8–13 mm. longis paullo infra medium decidue bracteolatis, cum calyce ferrugineo-hirsutis (pilis 0.2–0.3 mm. longis patentibus); calycis laciniis quatuor ovato-deltoideis, 1.7–2.2 mm. longis et latis, intus glabris, apice obtusis, postica curvata plicata oblongo-lanceolata, calcare excepto 18–22 mm. longa, expansa 8–10 mm. lata, calcare gracili subrecto 7–8 mm. longo; petalis jam delapsis non visis; stamine dense ferrugineo-sericeo (pilis ad 0.5 mm. longis), filamento crasso 1–1.5 mm. longo, anthera crassa (circiter 1.5 mm. diametro) 16–18 mm. longa, facie ventrali concava, apice obtuse conica; ovario dense sericeo, stylo crasso 14–17 mm. longo basin versus parce sericeo excepto glabro, stigmate subcapitato.

Type, *Pinkus 167*, collected January 22, 1939, in mixed forest along Maurukow Creek, headwaters of Rio Cotinga near Venezuelan boundary, drainage of Rio Branco, State of Amazonas, Brazil. The new species falls into the Series *Ferrugineae*, in which it seems most closely related to *V. majuscula* Pilger of Amazonian Peru, a species very similar to ours in foliage, but with a curved and conspicuously thicker calyx-spur and a glabrous ovary. Another close relative of the new species is *V. densiflora* Spruce of the Rio Uaupes region, but, in comparison with ours, that species has obovate leaves, secondary nerves which are straighter, more distant, and less spreading, and a much stouter calyx-spur.

EUPHORBIACEAE[1]

Mabea argutissima Croizat, sp. nov. Arbor gracilis ad 4 m. alta, innovationibus pube indutis sub lente crispule lanulosa, tomentum badium haud continuum efformante, serius glabritis, cortice laeviusculo brunneo; folia

[1] By L. Croizat.

exacte elliptica, apice subabrupte caudato-cuspidata, basi subrotundata, 5–9 cm. longa, 1.5–2.5 cm. lata, firme chartacea, brunneo-olivacea subconcoloria, pilis raris ad basin nervii medii exceptis tota glaberrima, margine primo intuito eroso, oculo armato eximie serrulato, dentibus adpressis ciliato-setaceis ad 7 per centimetrum, nervis circiter 10-jugis, more generis late patentibus laxe laqueatis, petiolo gracili circiter 3 mm. longo, hispidulo supra in apice obscurissime glanduloso, glandulis lente inquirendis, stipulis petiolaribus subtriangularibus setaceis, rectis vel apice incurvatis, margine laevissime glandulosociliatis, puberulis, ad 9 mm. longis; capsula ellipsoidea trigona, 1.6 cm. longa, 1.4 cm. lata, vix puberula, pericarpio coriaceo griseo laevissimo, in apice basi columnae stylaris indurata apiculata, calyce sub fructu 3 mm. lato, lobis triangularibus abrupte acuminatis, semine ellipsoideo, 7 mm. longo, 4 mm. lato, submaturo badio, laevissimo, raphide nigro perspicuo, columella fructu delapso 11 mm. longa.

Type, *Pinkus 275*, collected January 19, 1939, in the vicinity of Arabupu, Mount Roraima District, Venezuela, alt. 4200 ft., and deposited in the herbarium of the Arnold Arboretum (dupl. in Herb. N. Y. Bot. Gard., etc.). "Slender tree in second growth, 12 ft. high; trunk 5 in. diam.; fruit green." Although the type locality of *M. biglandulosa* Baill. is also the vicinity of Mount Roraima, the present species is easily distinguished from Baillon's. I have not seen an authentic specimen of *M. biglandulosa*, but Pax and Hoffmann (Pflanzenreich 4(147)[5]: 34. 1912) characterize it as "Arbor scandens; ramuli . . . glabri; . . . limbus . . . integer," which differentiates it from *M. argutissima*. It may be suspected that the new species belongs in the Section *Umbelluliferae* Pax & Hoffmann, but the material is too scanty to authorize even provisional statements. The combination of pubescence with a fine subaristate serration is not common in *Mabea*, according to the available material and the literature.

Cunuria Spruceana Baill. British Guiana: Membaru Creek, upper Mazaruni River, *Pinkus 236;* a tree in mixed forest, 70 ft. high; trunk 16 inches diameter; latex white. To the best of my knowledge the genus has not previously been reported from British Guiana, the four species thus far known being from the Rio Negro and Solimoes basins of Brazil. Compared with typical material of *C. Spruceana*, our specimens (in fruit) have slightly larger leaf-blades, which are truncate or faintly cordate at base, and larger capsules (to 6 cm. long).

Cunuria Gleasoniana Croizat, sp. nov. Arbor ad 20 m. alta, innovationibus sub lente hic inde pube nigrescente hispidulis, caeterum cortice glabrato crebre ruguloso sordide brunneo indutis, cicatricibus foliorum delapsorum 5 mm. longis et 3.5 mm. latis notatis; folia obovata vel elliptico-rotundata ad elliptica, 11–17 cm. longa, 7–8 cm. lata, coriacea, supra brunnea, subtus pube

brevissima arcte adpressa straminea interdum sublucida optime induta, basi subrotundato-cuneata, margine integra revoluta, trabeis conspicuis utrinque reticulatim venosa, venis penninerviis utrinque conspicuis interdum pilis simplicibus nigris tenuissimis, lente acri inquirendis, vestitis, 7–10-jugis, arcuato-adscendentibus, sub marginem ipsum tenuiter anatomosantibus, glandulis supra ad laminae basin 2 more generis late impresso-crateriformibus omnino sessilibus, petiolo valido toto ruguloso 1.5–3 cm. longo; inflorescentia ♂ haud visa sed ut videtur subapicali, forsan subgraciliter, paniculata vel cymulosa; inflorescentia ♀ subterminali (i. e. ex axillis ipsis summis) verosimiliter breviter spicato-cymosa ad 3 cm. longa, parcius adpresso-tomentosa, crassiuscula, ad 2 mm. basi diametiente, floribus 5–6 onusta; capsula submatura soluta tantum visa, epicarpio secedenti carnosula laevi, pube sericea more folii plus minusve induto, coccis solutis duris ad 18 mm. longis, semine immaturo laevissimo subtetragono rotundato ad 8 mm. lato, caruncula cerina magna, foveolis 4 circumambientibus in centro nempe cruciformibus.

Type, *Pinkus 176*, collected February 4, 1939, along Arubaru River (Kako tributary), upper Mazaruni drainage, near Mount Haiamatipu, British Guiana, alt. 2000 ft., and deposited in the herbarium of the Arnold Arboretum (dupl. in Herb. N. Y. Bot. Gard., etc.). Another collection is *Pinkus 234*, from Membaru Creek, upper Mazaruni River. The species is named for Dr. H. A. Gleason, in recognition of his important work on the flora of the region.

Although a definite identification of *Cunuria* requires full material, with staminate and pistillate inflorescences, there seems no doubt that this is the genus represented. The details of seed structure and capsule shown by Mueller (Mart. Fl. Bras. 11 (2): *pl. 14, f. 2*. 1874) fully agree with those of our plant. *Glycydendron* has an altogether different fruit. Of the known species of *Cunuria*, none seems to have the peculiar pubescence of *C. Gleasoniana*. The close, silky, pale yellow, and apparently fairly persistent indument of the lower surface of the leaf suggests that of certain Leguminoseae and is very rarely found in Euphorbiaceae. The scattered, very thin, blackish hairs sometimes found cloaking the midrib and the larger veins are also characteristic of the new species.

Croton roraimensis Croizat, sp. nov. Arbor ad 10–13 m. alta, trunco ad 30 cm. diametro, innovationibus pube sordida fasciculata, lepidibus subcrustaceis discoloribus taetris; folia subcoriacea firma brunneo-olivacea ovato-elliptica, 11–20 cm. longa, 4–9 cm. lata, sensim in apicem acuminata, basi subcuneato-rotundata, lepidibus argillaceis sparsis utrinque asperula, ex alabastro vix deprompta indumento cerino-lepidoto tota induta, adulta fere glabra, margine revoluto subsimpliciter crenato-serrato, dentibus subincurvis callosopuberulis ad 2 per centimetrum, nervo medio valido, venis lateralibus irregulariter circiter 7-jugis, modice patentibus, optime anatomosantibus, petiolo

valido 2.5–4.5 cm. longo tomentoso-hispido, subtus in apice glandulis utrinque 1 vel 2 ceraceis breviter stipitatis ornato, stipulis e basi lata setaceis integris rigidiusculis ad 8 mm. longis; cyma ♂: floribus conferte glomerulatis, pedunculo ad 8 mm. longo, rhachide ad 2 mm. crassa sub lente grosse tomentosa; calyce patente 1 cm. lato tenuissime tomentoso vel subglabro, lobis subovatis ad 4 mm. longis; petalis glabris, calycis lobis subaequilongis, circiter 1 mm. latis, margine laevissime ciliato-lanulosis; staminibus ad 20, basi pilosis, pro more generis minutis, vix 7.5 mm. longis; cyma ♀: calyce 8 mm. lato profunde partito vix accrescente, basi tomentello, supra glabrescente, stipite crassiusculo 2 mm. longo fulto, lobis late triangularibus ad 2 mm. longis, totidem ad basin latis; capsula pro more generis magna, 2 cm. longa, circiter 1.5 cm. lata, ellipsoidea, laevissime tantum trigona, tota tomento lepidoto subaureo induta, sub lente pilis fasciculatis hic inde hirtula, epicarpio crustaceo subtenui.

Type, *Pinkus 122*, collected January 6, 1939, on southwestern slopes of Mount Roraima, Venezuela, alt. about 7400 ft., and deposited in the herbarium of the Arnold Arboretum (dupl. in Herb. N. Y. Bot. Gard., etc.). Another collection from the same locality is *Pinkus 134*. The type is from a pistillate plant, the other collection from a staminate plant. It is a very distinct species, with affinities in the direction of *C. cuneatus* Kl., *C. surinamensis* Muell. Arg., and *C. matourensis* Aubl., from which it is easily distinguished by the elliptic or elliptic-ovate leaves, mostly rounded at the base, and by the indument. A close relationship is also suggested with the Peruvian *C. Tessmannii* Mansf., which, however, seems to be only remotely related to *C. hemiargyreus* Muell. Arg. as suggested by Mansfeld (Notizbl. Bot. Gart. Berlin 9: 265. 1927).

STERCULIACEAE

STERCULIA GUIANENSIS Sandwith. British Guiana: near Makreba Falls, Kurupung River, upper Mazaruni region, *Pinkus 15*. Excellent flowering specimens from the type locality.

OCHNACEAE[1]

Sauvagesia Imthurniana (Oliver) Dwyer, comb. nov. *Leitgebia Imthurniana* Oliver, Trans. Linn. Soc. II. 2: 271. 1887. *Roraimanthus Imthurnianus* Gleason, Phytologia 1: 39. 1933. Venezuela: Mount Roraima, summit, *Tate 400; Pinkus 116*. Mount Auyan-tepui, summit, *Tate 1130*.

All the characters of this plant indicate its position in the genus *Sauvagesia*, although previous workers have not considered it in relation to this genus. It is well marked specifically by its densely imbricate leaves and its flowers being borne on very short pedicels. The facts that the placentation of the ovary is parietal and that the staminodia of the inner

[1] In part by J. D. Dwyer.

corona are free to the base are verified by a careful examination of new and earlier material; thus the necessity for the genus *Roraimanthus* ceases to exist. Although it bears a superficial resemblance to *Leitgebia guianensis* Eichl. in having the leaves densely imbricate, the present plant differs in having the ovules attached basally and in lacking the outer ring of spatulate staminodia.

S. Imthurniana resembles *S. fruticosa* Mart. & Zucc. in the type of leaf, which is coriaceous and imbricate, with prominent, strongly ascending, striate veins.

Ouratea mazaruniensis A. C. Smith & Dwyer, sp. nov. Frutex vel arbor parva ubique glabra; ramulis teretibus crassis cinereis juventute plus minusve striatis; petiolis rugosis valde incrassatis (2–3 mm. diametro) 1–4 mm. longis; laminis tenuiter coriaceis vel chartaceis siccitate olivaceis vel fuscis, plus minusve concoloribus et supra interdum nitidis, elliptico- vel ovato-oblongis, (5–)7–12.5 cm. longis, 2.5–5 cm. latis, basi plerumque subcordatis interdum rotundatis vel late obtusis, apice rotundatis vel obtusis interdum emarginatis, margine regulariter et inconspicue crenulato-serratis (serrationibus 6–9 per centimetrum obscure calloso-apiculatis), costa supra elevata subtus prominente, nervis secundariis utroque 7–12 arcuatis marginem versus valde adscendentibus subtus prominulis supra subimmersis, venulis supra obscuris subtus paullo prominulis vel planis; paniculis pauciramosis terminalibus vel subterminalibus ad 10 cm. longis (quam foliis apicem ramulorum versus paullo longioribus); bracteis papyraceis oblongis acutis 3–6 mm. longis vel interdum foliaceis; pedicellis gracilibus sub anthesi curvatis 7–10 mm. sub fructu rectis ad 13 mm. longis; sepalis oblongo-ellipticis, 6–7.5 mm. longis, 2.5–3.5 mm. latis, apice obtusis vel minute apiculatis, exterioribus coriaceis interdum anguste scarioso-marginatis, interioribus praeter lineam medianam dorsalem coriaceam membranaceis luteis; petalis luteis tenuiter papyraceis vel membranaceis, late obovatis, 6–7.5 mm. longis, 5–7 mm. latis, basi valde contractis, apice rotundatis et interdum leviter emarginatis, conspicue nervatis, venulis flabellatim recurvatis; antheris sessilibus luteis subulatis valde transverse rugosis 5–6 mm. longis; gynophoro cylindrico sub anthesi 1–1.2 mm. longo et 0.7–1 mm. diametro; carpidiis 5 ovoideis 0.5–0.9 mm. longis; stylo gracili 4–5 mm. longo truncato; gynophoro sub fructu obovoideo ad 7 mm. longo et 4 mm. diametro; drupis paucis (saepe solitariis) oblongo-ovoideis ad 8 mm. longis et 6 mm. latis.

Type, *Pinkus 185*, collected February 2, 1939, along Arubaru River (Kako tributary), upper Mazaruni drainage, near Mount Haiamatipu, alt. about 2000 ft., British Guiana. Another collection from the same region is *Pinkus 278*. The new species is characterized by its short-petiolate leaves (appearing at first glance subsessile), of which the blades are usually rounded at apex and lightly cordate at base. It appears to be without close relatives, but in foliage may be compared with the Brazilian *O. glaucescens*

(St. Hil.) Engl., a species with a simpler inflorescence, stouter pedicels, slightly larger flowers, and more numerous carpels. On the basis of inflorescence characters the new species is doubtless more closely related to such species as *O. roraimae* Engl. and *O. rigida* Engl., but these are very different in foliage.

CARYOCARACEAE

ANTHODISCUS OBOVATUS Benth. British Guiana: Membaru Creek, upper Mazaruni region, *Pinkus 233;* Arubaru River (Kako tributary), upper Mazaruni drainage, near Mount Haiamatipu, *Pinkus 280.* The species is apparently new to Guiana, having previously been known from the Rio Negro region of Brazil. Our specimens have the leaflets conspicuously emarginate at apex, the flowers large (petals to 9 mm. long; filaments to 7 mm. long), and the immature fruits smooth rather than sulcate. However, they seem to fall into a reasonable concept of the species.

THEACEAE

ARCHYTAEA MULTIFLORA Benth. British Guiana: Arubaru River (Kako tributary), Mazaruni drainage, near Mount Haiamatipu, alt. about 2000 ft., *Pinkus 175.* Hitherto known from Mount Roraima, Mount Duida, and adjacent Brazil.

GUTTIFERAE

CLUSIA MELCHIORI Gleason. Venezuela: Mount Roraima, southwestern slopes, in damp forest, alt. about 7400 ft., *Pinkus 161.* Previously known from Mount Duida; like the type, our specimen bears young fruits.

Tovomita albiflora A. C. Smith, sp. nov. Arbor glabra ad 8 mm. alta, ramulis conspicue rugosis subteretibus vel apicem versus compressis; petiolis crassis 1.5–3 cm. longis basi incrassatis ut ramulis rugosis et mox saepe purpurascentibus; foliorum laminis chartaceis ellipticis, (9–)12–20 cm. longis, (3–)4–6.5 cm. latis, basi acutis vel subattenuatis, apice acutis vel obtuse et breviter cuspidatis, margine cartilagineis integris, supra viridibus, subtus saepe paullo pallidioribus, costa valida utrinque prominente et striata, nervis lateralibus primariis utroque 9–13 arcuatis marginem versus (2–3 mm.) abrupte curvatis et inconspicue anastomosantibus, nervis secundariis lateralibus paucis inconspicuis, venulis copiose reticulatis utrinque prominulis; inflorescentiis masculis terminalibus sessilibus multifloris ad 3 cm. longis et 5 cm. latis, e basi 4- vel 5-ramosis, ramulis primariis 9–13 mm. longis valde compressis 2–4 mm. crassis rugosis conspicue lenticellatis, in cymas 3-floras desinentibus; bracteis tenuiter coriaceis oblongis acutis 5–7 mm. longis; pedicellis crassis (circiter 2 mm. diametro) rugosis 3–6 mm. longis, 2 lateralibus basin versus articulatis et bibracteolatis (bracteolis papyraceis oblongo-ovatis carinatis, circiter 4 mm. longis, apice subacutis, basi alte connatis); sepalis 4 chartaceis, 2 exterioribus semiorbiculari-ovatis, 4–5 mm. longis et latis, apice rotundatis,

florem involventibus, 2 interioribus oblongis, 2–3 mm. latis; petalis 4 tenuiter carnosis oblongis, 4–5 mm. longis, 2–3 mm. latis, apice rotundatis; staminibus 40–45, 3–4.5 mm. longis, filamentis crassis (0.5–0.6 mm. diametro), antheris 0.5–0.6 mm. longis, quam filamentis haud latioribus; inflorescentiis femineis 3–6 cm. longis et latis, 9–15-floris, pedunculatis (pedunculo 8–15 mm. longo), ramulis primariis 3 et pedunculo inflorescentiarum masculorum ramulis similibus; bracteis bracteolis et perianthio eis florum masculorum similibus sed paullo majoribus (pedicellis ad 8 mm. longis, petalis ad 7 mm. longis et 4 mm. latis); staminodiis staminibus similibus; ovario cylindrico conspicue striato, stigmatibus 4 conspicuis subsessilibus subpeltatis; fructibus subpyriformibus coriaceis rugosis conspicue lenticellatis, maturitate 3–3.5 cm. longis et 1–1.5 cm. diametro, basin versus contractis, apice attenuatis, stylis 4 crassis brevibus connatis sub stigmatibus articulatis; reliquis floris sub fructu saepe persistentibus.

Type, *Pinkus 269*, collected January 19, 1939, in the vicinity of Arabupu, Mount Roraima District, Venezuela, alt. 4200 ft. The collector reports that the Arekuna name is "wakome," and that the flowers are fragrant, with white petals and stamens. *T. albiflora* closely resembles *T. rubella* Spruce, from the Rio Negro of Brazil, in its leaf-texture and venation, but has the leaf-blades more distinctly elliptic and less gradually tapering at base. The most distinguishing characters of the new species are found in the stout rugose lenticellate inflorescence-branches and the short stout pedicels; these features contrast with the smooth and slender corresponding parts of *T. rubella*, which also has fewer stamens than the new species. Another species of this relationship is *T. calodictyos* Sandwith, of British Guiana, which has the leaves essentially similar but with 16–22 primary lateral nerves, smooth inflorescence branches, and fewer stamens.

PASSIFLORACEAE[1]

Passiflora Cardonae Killip. British Guiana: Membaru Creek, upper Mazaruni River, *Pinkus 38*. Previously known only from the type collection from Mount Auyan-tepui, Venezuela.

MELASTOMATACEAE[2]

Miconia megaphylla Gleason. British Guiana: Adaro River (Kukui tributary), upper Mazaruni drainage, near Mount Wupaima, *Pinkus 164*. New to British Guiana; previously known only from subandean Bolivia.

MYRSINACEAE

Conomorpha sessilis A. C. Smith, sp. nov. Arbor ad 5 m. alta, trunco ad 15 cm. diametro; ramulis subteretibus cinereis juventute densissime et arctissime ferrugineo-tomentellis mox glabris; petiolis 12–18 mm. longis supra

[1] By E. P. Killip.
[2] By H. A. Gleason.

leviter canaliculatis juventute ut ramulis tomentellis; laminis chartaceis vel tenuiter coriaceis siccitate subglaucis vel fuscis oblongo- vel leviter obovato-oblongis, 8–10.5 cm. longis, 3–4.5 cm. latis, basi acutis et in petiolum decurrentibus, apice cuspidatis vel breviter acuminatis (acumine 5–10 mm. longis obtusis), margine integris et anguste sed conspicue revolutis, supra punctulis innumeris nigris obscure obtectis, subtus dense ferrugineo-lepidotis, costa supra leviter insculpta subtus prominente, nervis secundariis numerosis (utroque 15–20) leviter arcuatis et marginem versus anastomosantibus utrinque haud prominulis; inflorescentiis subpyramidatim paniculatis 3–4 cm. longis ubique praeter corollam densissime ferrugineo-lepidotis; pedicellis 0.8–1.2 mm. longis; calycis lobis fere ad basin liberis 4 vel 5 oblongo-deltoideis, 0.7–0.9 mm. longis, subacutis, parcissime punctatis, intus glabris; corolla lutea glabra 2–2.2 mm. longa, lobis 4 (raro 5) ovatis, circiter 1.3 mm. longis et latis, apice obtusis, basi leviter contractis, parcissime nigro-punctatis; staminibus basi corollae loborum insertis, filamentis subnullis, antheris luteis oblongo-deltoideis 0.8–0.9 mm. longis dorso parcissime glandulosis; ovario sub anthesi circiter 0.5 mm. diametro pallide lepidoto, stylo crasso circiter 1 mm. longo truncato.

Type, *Pinkus 55*, collected December 12, 1938, along Arabupu River near Arabupu, Mount Roraima District, Venezuela, alt. 4200 ft. *C. sessilis* appears to be most closely related to *C. punctata* Mez, also of the Mount Roraima region, from which it differs in its narrower and thicker leaves, shorter pedicels, smaller and usually 4(rather than 5- or 6)-merous flowers, and its even less conspicuous filaments. The specific name refers to the essentially sessile anthers.

Conomorpha gracilis A. C. Smith, sp. nov. Arbor ad 7 m. alta, trunco ad 15 cm. diametro; ramulis crassis cinereis subteretibus juventute arctissime cano-pulverulentibus mox glabris; petiolis subteretibus gracilibus 12–20 mm. longis mox glabris; laminis tenuiter coriaceis siccitate utrinque viridibus vel olivaceis ellipticis vel obovato-ellipticis, (4–)6–9 cm. longis, (2–)3–5 cm. latis, basi acutis vel attenuatis et in petiolum decurrentibus, apice obtusis vel rotundatis et saepe minute emarginatis, margine integris et leviter recurvatis, utrinque glabris, supra punctulis paucis nigris obscure obtectis, subtus dissite et immerse punctulatis, costa valida supra elevata subtus prominente, nervis secundariis utroque 12–18 patulis prope marginem anastomosantibus cum rete venularum utrinque valde prominulis; inflorescentiis racemosis 4–10.5 cm. longis 20–35-floris breviter stipitatis, cum foliis apices ramulorum versus congestis, ubique praeter corollam parce ferrugineo-puberulis; bracteis linearioblongis 1.3–1.8 mm. longis; pedicellis 1–2 mm. longis; calyce cupuliformi circiter 1.3 mm. longo, lobis 4 deltoideo-ovatis, circiter 0.9 mm. longis et 1.1 mm. latis, apice obtusis, margine integris et minute ciliolatis, intus glabris, obscure punctulis nigris paucis (2 vel 3 per lobum) pictis; corolla lutea 3.5–4.5 mm. longa basin versus glabra, lobis 4 oblongis, 1.8–2.6 mm. longis, 1.4–2.2 mm.

latis, apice obtusis, intus dense papilloso-puberulis, extus glabris vel parcissime puberulis; staminibus basi corollae loborum insertis, filamentis complanatis circiter 0.5 mm. longis, antheris oblongo-deltoideis, 1.1–1.3 mm. longis, saepe recurvatis, basi cordatis, apice obtusis; ovario dense pallide lepidoto conico sub anthesi 0.5–0.7 mm. diametro, stylo gracili 1–1.5 mm. longo apice leviter incrassato.

Type, *Pinkus 181*, collected February 2, 1939, along Arubaru River (Kako tributary), upper Mazaruni drainage, British Guiana, alt. about 2000 ft. In the essential characters of the long racemose inflorescences, large 4-merous flowers, obvious filaments, lepidote ovary, and slender tapering style, *C. gracilis* resembles *C. grandiflora* Mez, of the Rio Negro region of Brazil, doubtless its closest ally. The new species differs from *C. grandiflora*, however, in its proportionately broader leaves, which are concolorous rather than reddish beneath and which have a more conspicuous venation. The calyx-lobes of *C. grandiflora* are proportionately longer than those of *C. gracilis* and more obviously punctate. The specific name of the new species refers to the long slender inflorescence.

Rapanea roraimensis A. C. Smith, sp. nov. Arbor glabra ad 10 m. alta, trunco ad 20 cm. diametro; ramulis subteretibus cinereis striatis; petiolis rugosis 7–10 mm. longis supra leviter canaliculatis superne anguste alatis; laminis chartaceis siccitate olivaceis concoloribus anguste ellipticis, 11–16 cm. longis, 3–5 cm. latis, basi attenuatis, apice acutis (apice ipso saepe obtuso et mucronulato), margine integris et leviter recurvatis, utrinque inconspicue et dispersissime punctatis, costa supra elevata et leviter canaliculata subtus prominente et striata, nervis secundariis utroque 12–20 subpatulis cum rete venularum conspicuo irregulariter anastomosantibus et utrinque prominulis; inflorescentiis fasciculatis vel e ramulis verruciformibus (pedunculo crasso ad 4 mm. longo) 5–10-floris formatis; bracteis deltoideis 1–1.3 mm. longis subacutis minute ciliolatis; florum femineorum pedicellis rugosis crassis 1.3–2.6 mm. longis; calyce erecto-patente, lobis 5 fere ad basin liberis deltoideo-ovatis, 0.7–0.9 mm. longis et latis, apice obtusis vel rotundatis, margine minute ciliolatis, parce nigro-punctatis et interdum lineolatis; corolla subrotata sub anthesi 3.5–4.5 mm. diametro, lobis 5 elongato-deltoideo-oblongis, 1.5–1.8 mm. longis, 0.8–1.1 mm. latis, apice obtusis, margine minute puberulo-ciliolatis, dense fusco-glanduloso-lineolatis; staminibus quam corollae lobis paullo brevioribus, antheris sessilibus oblongis 1–1.2 mm. longis, basi sagittatis, apice subacutis; ovario laevi glabro cylindrico, circiter 1.3 mm. longo et 0.9 mm. diametro; stigmate cylindrico circiter 1.5 mm. longo, apice irregulariter lobato-crenato.

Type, *Pinkus 132*, collected January 11, 1939, in damp forest on southwestern slopes of Mount Roraima, Venezuela, alt. about 7800 ft. The new species is characterized by its glabrous habit, chartaceous nar-

rowly elliptic leaf-blades with prominulous venation, and comparatively long pedicels. Among the species known to me from herbaria, descriptions, and Mez's treatment in the Pflanzenreich, it seems most closely related to *R. lancifolia* (Mart.) Mez and *R. umbellata* (Mart.) Mez, both of southern Brazil. From the former it differs by its larger leaves and flowers and narrower corolla lobes, from the latter by its thinner, duller, and somewhat more pointed leaf-blades, and its shorter pedicels. Although *R. roraimensis* bears a slight resemblance to some of the specimens placed with *R. guyanensis* Aubl. in herbaria, it obviously differs in many respects from the typical form of that species, which has thick obovate-elliptic leaf-blades with immersed venation and rounded or obtuse apices, and very short pedicels.

Rapanea resinosa A. C. Smith, sp. nov. Frutex glaber ad 1 m. altus; ramulis subteretibus striatis juventute castaneis demum cinereis; petiolis rugosis 5–10 mm. longis superne anguste alatis; laminis chartaceis siccitate fusco-olivaceis concoloribus lineari-ellipticis, 5–11 cm. longis, 1.3–3 cm. latis, basi attenuatis, apice gradatim acutis (apice ipso saepe obtuso et calloso), margine leviter recurvatis et integris vel apicem versus leviter crenulatis, utrinque plerumque lineis resiniferis perlongis (saepe obscure) auctis et dispersе (supra impresso-) punctatis, costa supra elevata subtus prominente, nervis secundariis utroque 8–12 subrectis adscendentibus utrinque prominulis, rete venularum plerumque inconspicue prominulo; inflorescentiis fasciculatis vel e ramulis verruciformibus (pedunculo ad 2 mm. longo) 7–15 floris formatis; bracteis deltoideis circiter 1 mm. longis subacutis ciliolatis; pedicellis crassis 2–3 mm. longis; floribus masculis: calyce patente, lobis 5 fere ad basin liberis ovato-deltoideis, 0.9–1.1 mm. longis et latis, apice subacutis vel obtusis, margine minute et regulariter glanduloso-ciliolatis, parce nigro-punctatis (punctulis 2–6 per lobum); corolla rotata sub anthesi 6–7 mm. diametro, lobis 5 (raro 6) oblongis, 2.2–3 mm. longis, 1.3–1.5 mm. latis, apice obtusis vel rotundatis, margine minute puberulo-ciliolatis, parce nigro-punctatis (punctulis saepe paullo elongatis sed haud lineolatis); staminibus quam corollae lobis brevioribus, antheris sessilibus oblongo-ovoideis, 1.7–2 mm. longis, obtusis, crassis; ovario laevi conico, stigmate sessili punctiformi; floribus femineis: corolla quam mascula paullo minore, lobis 1.7–2 mm. longis, haud punctulatis; antheris elongato-deltoideis circiter 1 mm. longis, basi sagittatis, apice subacutis; ovario subgloboso sub anthesi 1–1.5 mm. diametro, minutissime aureo-glanduloso; stigmate sessile morchelliformi ovarium subaequante; fructibus subglobosis atris 3–4 mm. diametro, stigmate persistente coronatis.

Type, *Pinkus 84*, collected January 17, 1939, along Arabupu River, near Arabupu, Mount Roraima District, Venezuela, alt. 4200 ft.; flower buds greenish, streaked with red. *R. resinosa* is characterized by its glabrous habit and its leaf-blades with resinous lines. Its relationship is with

the Brazilian *R. umbrosa* (Mart.) Mez, from which it differs only in minor details, such as slightly narrower leaf-blades, longer pedicels, and calyx- and corolla-lobes which are not glandular-lineolate. The new species bears a superficial resemblance to the widespread and variable *R. ferruginea* (R. & P.) Mez, but that species has tomentellous young branchlets and a glandular-lineolate perianth, and lacks the resinous lines in the leaf-blades.

APOCYNACEAE[1]

HIMATANTHUS PHAGEDAENICA (Mart.) Woodson. Venezuela: Mount Roraima District, vicinity of Arabupu, alt. 4200 ft., *Pinkus 168*. New to Venezuela; otherwise known from Brazil, from the Rio Negro basin southward to Rio de Janeiro.

RUBIACEAE[2]

CEPHAELIS TATEI Standley. British Guiana: Membaru Creek, upper Mazaruni River, *Pinkus 228*. Previously known from Arabupu, Mount Roraima District, Venezuela.

LADENBERGIA PITTIERI Standley. British Guiana: Adaro River (Kukui tributary), upper Mazaruni drainage, near Mount Wupaima, alt. about 3000 ft., *Pinkus 170*. Previously reported from Andean Venezuela and eastern Colombia.

Psychotria mazaruniensis Standley, sp. nov. Arbor 6-metralis, trunco 7.5 cm. diam., omnino glabra, ramulis gracilibus teretibus in sicco fere nigris atque infra nodos valde constrictis; stipulae persistentes erectae 7–9 mm. longae inferne in vaginam connatae, parte libera utroque latere biloba, lobis vagina brevioribus obtusis vel subrotundatis atque setoso-mucronatis; folia magna petiolata firme membranacea, petiolo gracili 2–2.5 cm. longo; lamina oblongo-ovalis 15–20 cm. longa 6.5–9 cm. lata apice rotundata atque subito cuspidata, acumine anguste attenuato acuto 1–1.5 cm. longo, basi acuta atque interdum subito contracta, supra in sicco intense olivacea lucida, costa prominula, nervis venisque quoque prominulis vel prominentibus, subtus vix pallidior, sublucida, costa gracili elevata, nervis lateralibus utroque latere ca. 16 prominulis angulo fere recto abeuntibus arcuatis, nervis aliis fere aequaliter prominentibus inter pares adjectis, venulis prominulis laxe reticulatis; inflorescentia terminalis erecta 6 cm. longe pedunculata ca. 4 cm. longa, floribus capitatis, capitulis 5 racemosis dense multifloris breviter pedunculatis ca. 1 cm. diam., bracteis extimis ovato-rotundatis apice late obtusis vel rotundatis adpressis glabris; calyx brevis, margine angulato vel brevissime remote denticulato; corolla alba extus glabra, tubo 8–10 mm. longo crassiusculo infra orem subconstricto, lobis brevibus oblongis obtusis recurvis, extus apice appendice albo papilloso auctis.

[1] By R. E. Woodson.
[2] By P. C. Standley.

Type, *Pinkus 14*, collected September 13, 1938, on rocky soil on hillside, Kurupung Mountain, near Makreba Falls, upper Mazaruni region, British Guiana, and deposited in the herbarium of the Field Museum (dupl. in Herb. N. Y. Bot. Gard., etc.). The corollas in bud are exserted far beyond the bracts. They bear at the apex small, rounded, whitish appendages that afford a striking character for recognition of the species. The plant might be referred equally well, perhaps, to the genus *Cephaelis*.

COMPOSITAE[1]

QUELCHIA CONFERTA N. E. Brown. Venezuela: Mount Roraima, summit, alt. 8700 ft., *Pinkus 112;* shrub 3 ft. high; pappus white. Apparently only the second known collection of this endemic monotype. The only corollas on the type material were in bud, and Brown's description does not apply to the mature ones. In these the proper tube is slenderly obconic, rather sparsely pilosulous outside with loose several-celled hairs, and 4 mm. long; the throat is practically lacking, the filaments being inserted only about 0.3 mm. below the apex of the tubular part of the corolla; the 5 equal lobes of the limb are recurved-spreading, linear, obtusish, 5 mm. long. The tails of adjacent anthers are connate for about half their length and are sparsely hispidulous-barbate. The copious whitish-straw-colored pappus bristles are somewhat flexuous, about 3-seriate, hispidulous especially toward base, and somewhat stramineous toward base; they are subequal, with the exception of a very few short outermost ones about 2 mm. long. The style branches are about 1 mm. long, glabrous, oblong, somewhat widened toward the truncate bluntly 2–3-toothed apex, with recurved-spreading tips.

Stenopadus condensatus (Baker) Blake, comb. nov. *Stifftia condensata* Baker in Mart. Fl. Bras. 6 (3): 351. 1884. Venezuela: Mount Roraima, southwestern slopes, alt. about 7200 ft., *Pinkus 157;* shrub 1 ft. high, growing among rocks in open places; bracts and anthers yellowish. The specimens agree well with Baker's description and with a scrap in the U. S. National Herbarium collected by Jenman (no. *10*) in "high stony ground, near Waetipoo M., Cotinga R.," on the Mt. Roraima expedition of 1884–85. The Jenman specimen has broader, obovate leaves, up to 23 × 13 mm., but the differences observed are within the ordinary range of variation of species in this group. A single receptacular pale was found in one of the two heads of the sheet of Pinkus' plant examined, confirming the reference of the species to the genus *Stenopadus*. It is very narrowly linear, 22 mm. long and barely 0.5 mm. wide, somewhat conduplicate, acute, minutely hispidulous-ciliolate toward the tip.

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[1] By S. F. Blake.

Straussia sessilis, a New Species from Hawaii

Otto Degener and E. Y. Hosaka

Rubiaceae are well represented in the Hawaiian Islands. The following species is here described as new:

Straussia sessilis Degener & Hosaka, sp. nov. Paniculis 5–10 mm. longis, corollis glabris et calicibus puberulis.

A small tree 3–7 meters high with leaves clustered at the ends of reddish-brown branches. Leaves glossy, 7–12 cm. long and 3.5–7 cm. wide, on petioles 5–10 mm. long, obovate, entire, glabrous above, sparsely puberulent chiefly between the veinlets below, somewhat obtuse at apex, somewhat acute at base; stipules 4–5.5 mm. long, broadly ovate, obtuse at apex, coriaceous, entire, glabrous on outer surface, densely pilose on inner surface below the middle, caducous. Flowers sessile, usually 10–20 crowded together into a branched cluster about 1.5 cm. high and 2–3 cm. wide having axis 5–10 mm. long, hidden by persistent fleshy stipules. Calyx green, puberulent, 3 mm. wide, 3–5 mm. long with the free 2 mm. limb unevenly and obscurely 5- to rarely 6-toothed, thick. Corolla white, thick, glabrous throughout, about 15 mm. wide, its tube 2–3 mm. long and its acute lobes about 4 mm. long, with throat naked. Free part of filament 1.5 mm. long, glabrous, white; anthers yellow, 1 mm. long; pollen yellow. Ovary 1.5 mm. long, 2 mm. wide, glabrate, whitish; style 2-branched, pubescent, green. Fruit orange, with prominent longitudinal ridges when dried, 10–15 mm. long, 8–10 mm. wide, with exposed obtuse disk about 2 mm. long and 5 mm. wide.

Type locality: North of head of Makua Valley, Oahu. This forest tree, called *kopiko* by the natives, is known only from the Waianae Range of the Island of Oahu, growing here and there north of Mt. Kaala. It is closely related to *S. oncocarpa* Hilleb. *S. sessilis* has a glabrous panicle 5–10 mm. long, a sparsely puberulent calyx and a glabrous corolla; *S. oncocarpa*, on the other hand, has a rusty-pubescent panicle 2.5–5 cm. long and rusty-pubescent calyx and corolla. This new *kopiko* was collected by Forbes (*No. 1808*) on the "slope of Kaala, Mokuleia," April–May, 1912; by Hosaka (*No. 1129 A*) "in semi-moist forest, el. 1700 ft., Mokuleia, Waialua," August, 1933; and by Degener & Salucop (*No. 11,525*) "north of head of Makua Valley, in rain-forest," October 24, 1937. This specimen and thousands of others upon which descriptions for the *Flora Hawaiiensis* or "New Illustrated Flora of the Hawaiian Islands" are based comprise the Degener Herbarium, now deposited on loan at the B. P. Bishop Museum, under the directorship of Dr. Peter Buck. The most complete duplicate set belongs to the New York Botanical Garden.

Waialua, Oahu.

Origin and Development of the Uniseriate Ray in the Coniferae

Elso S. Barghoorn, Jr.

(with 24 figures)

The extensive literature of the anatomy and morphology of the Coniferae[1] contains no complete data on the origin and ontogeny of their ray tissue. It is my intention to review briefly the previous work and to endeavor to clarify certain incompletely investigated points.

1. *Origin of Ray Initials.* The first writers on the details of the origin of cambial ray initials allude to the obscurity of the process (Müller, 1875; Velten, 1875; De Bary, 1884). Müller and Velten made the first efforts to explain the spatial relationships between newly-formed ray initials and the fusiform initials from which they originate. Schmidt (1889) concluded that wood rays of the conifers arise in the cambium by division of fusiform initials. His work, like Müller's and Velten's, was not essentially critical and was not concerned with the cytological mechanism involved. Later, Klinken (1914) in a study of cambial activity in *Taxus baccata* L. affirmed Schmidt's results, but without cytological data. His evidence from serial tangential sections of coniferous phloem was in accord with that which Schmidt obtained from radial sections of the xylem. Thompson's work (1910) was not concerned with the origin and ontogeny of ray tissue in general. This is true also of Chrysler's researches (1913) on the phloem of Pinaceae. Both investigated mature structures and did not deal with phenomena in the cambium.

2. *Ontogeny of Ray Tissue.* Several critical studies have been made of the ontogeny of coniferous rays. That of Jost (1901) is among the earliest, though previously Kny (1884) had noted the marked difference in height of rays between the first annual ring and the older wood of *Pinus sylvestris*. Jost was concerned chiefly with the adjustments of the cambium in the crotch regions of coniferous and dicotyledonous trees. He found that in these regions of pressure and tension the cambium decreased in area, but that individual rays continued to undergo a normal ontogeny as further increments were added.

Klinken, on the other hand, found that by loss of ray initials in the cambium a decrease in height of the rays of *Taxus baccata* might occur. Klinken also confirmed the observations of Zijlstra (1908) and Jost on the splitting of rays by elongating fusiform initials in the cambium.

[1] Nomenclature of Pilger (1926).

Thompson and Holden (1913) and Chrysler (1913, 1915) concerned themselves chiefly with the study of mature xylem and phloem and offered no interpretation of ray ontogeny in terms of cambial activity.

More recently Bannan (1934) made an extensive survey of the different cell types associated with ray origins in representative species of Coniferae and other gymnosperms. He concluded that ray initials "evidently are formed by segmentation of fusiform initials." He did not, however, elaborate upon the details of the process or the cambial changes involved.

In general it may be said that previous researches have dealt with special aspects of these problems and no organized synthesis has yet been made. Much of the work was hampered by preconceived conclusions about the phylogeny of the conifers. Because of this phylogenetic bias, ontogenetic studies were neglected and interpretation was based largely upon a study of mature structures. It should be emphasized that in comparative anatomical work valid phylogenetic conclusions cannot be drawn until ontogenetic processes are reasonably well understood. The following study is primarily concerned with the origin and ontogeny of ray tissue.[1]

MATERIALS AND METHODS

For the most part the technique was that usual in anatomical research. In addition a method was devised whereby large quantities of material might be rapidly and effectively studied. In dealing with fresh, living material fixation and dehydration consume much time and often destroy or obscure detail present in the untreated tissues. A method that employs only aqueous media is therefore preferable. Water-soluble aniline blue as recommended by Crafts (1931) is one of the most satisfactory of these. Instead of glycerin or glycerin jelly commercial corn syrup (Karo) was used for permanent mounts (Monk, 1938). In this way serial tangential sections of xylem or phloem were prepared in a fraction of the time required for dehydration. If the tissues must be stained to render cellular details more plainly visible, safranin added to the water or alcohol used in sectioning is satisfactory. Sections thus prepared are stained on the knife or on the slide just preparatory to mounting. Water-soluble nigrosin is an alternative stain particularly satisfactory for sections of celloidin-embedded woody tissue mounted in corn syrup. Difficulties that arise from a tendency of the stain to clot on the sections after the addition of corn syrup may be overcome by placing the slides over night or for several days in an incubator at 55–60° C. This promotes a more rapid diffusion of the stain and hastens the drying of the slides.

[1] Canal-bearing rays of both conifers and dicotyledons will be treated separately in a later study.

As previously mentioned, it is not possible by a study of the xylem alone to reconstruct accurately the cytological changes involved in the formation of new ray initials. The more or less extensive apical growth of differentiating tracheids markedly alters the cellular relations which existed in the cambium. Also the xylem-forming divisions of newly formed ray initials and of marginal ray initials are frequently sporadic. The xylem derivatives of such initials are therefore spaced at varying distances and do not form radially contiguous series of cells which can be traced in serial tangential sections. In the phloem, on the other hand, there is very little extra-cambial elongation of daughter cells, except for certain fibers, and the phloem derivatives of ray initials are always in series of contiguous cells. In serial tangential sections it is therefore possible to reconstruct the changes which resulted from successive divisions in the cambium.

After a careful study of serial tangential sections the interpretation of radial sections of both xylem and phloem is far more accurate.

ONTOGENETIC STAGES

Ray Origins in the Primary Body

In the primary body of the conifers a definite relation exists between the number of rays that originate in the fascicular and in the interfascicular regions of the stele.[1] As is shown in figure 1, a higher proportion of rays originates in the latter. The anatomical-physiological significance of this relation is not clear, since there are no "foliar rays" or structures in any way related to them in living conifers. However, the existence of such a relation bears directly on the problem of ray ontogeny, since there are distinct differences in size and shape between ray cells that originate in the two different regions. In the interfascicular segments, between the discontinuous protoxylem points of the stem, certain vertically elongated parenchymatous cells are rapidly continuous with the parenchymatous (or tracheary) cells of the wood ray. It would seem, therefore, that certain cells of this so-called medullary crown region give rise to the cambial ray initials, which in turn give rise to the ray tissue of the secondary body. Such "primary ray cells"[2] are vertically elongated and more or less regularly rectangular. This is generally true also of the "primary ray cells" that originate in the fascicular segments of the primary xylem. However, in these segments the parenchymatous cells which give rise to ray initials are much more elongated vertically and are

[1] In dealing with the primary body the terms fascicular and interfascicular are here used respectively for the primary xylem strands and the intervening parenchymatous tissue.

[2] The term "primary ray cell" refers to those cells of the primary body which, by periclinal division, give rise to ray initials.

arranged in extensive vertical strands closely appressed between the protoxylem tracheids of the primary wood. This position, and the occurrence of the component cells in vertically contiguous series, support the view that the "primary ray cells" of the fascicular segments are derived from the elongated cells of the procambial strands by a series of anticlinal divisions.

There is, therefore, a definite ontogenetic factor in the two types of primary ray origins. "Primary ray cells" that arise in the interfascicular gaps are derived from certain primordial cells of the growing point which did not undergo extensive vertical elongation. In the other type, the "primary ray cells" in the fascicular segments are apparently derived from vertically elongated procambial cells by a series of anticlinal divisions.

The distinction between these two types of primary ray origins is of great importance in the transition from primary to secondary tissue. This is particularly true of the dicotyledons, in many of which the broad multiseriate rays of the secondary body are definitely related to the interfascicular gaps of the primary body. In the conifers, however, the transition to secondary tissue is similar in both the fascicular and interfascicular regions. All the first-formed ray cells of the secondary wood betray a rapid and extensive change in cell size and shape during differentiation. The degree of this change varies greatly in different species, but the qualitative nature of the change is the same in all the Coniferae. The first ray cells that are unquestionably of secondary origin are frequently highly irregular in outline and more or less radially elongated. Elongation occurs independently of the surrounding tissue and tends to separate each cell of a ray from the neighboring component above or below. Thus a series of rays, one, two, or three cells in height, originates from the strand of vertically contiguous members of the primary ray tissue. Also, certain "primary ray cells" fail to divide periclinally and thereby further disrupt the potential vertical extent of the newly-formed rays of the secondary xylem. Two factors are thus involved in the formation of the very low uniseriate rays of the young stem wood of conifers:

(1) the independent development of individual ray initials in the originally vertically contiguous series and

(2) the failure of certain "primary ray cells" in the vertical series to give rise to secondary ray initials.

In the roots the wood rays of corresponding young regions of the secondary axis tend to be considerably higher and frequently more abundant. The increased height is due to a modification of the above two factors. The transition from vertically elongated "primary ray cells" to radially elongated secondary ray cells takes place more slowly. This allows time

for the occurrence in the ray initials of transverse anticlinal divisions which tend to retain the vertical continuity between the individual cells of the ray. Of secondary importance is the greater prevalence of periclinal divisions in the "primary ray cells" of the root than in those of the stem. The quantitative importance of these two factors, which bring about the difference in ray structure of root and stem, varies in different conifers.

The very irregular shape of certain coniferous rays cells has been frequently noted. In general this plasticity of cell form is greatest in the first few annual rings of roots (Figs. 4 and 12) where it may well be considered a concomitant of the peculiar transition from primary to secondary ray tissue. In the change from the "primary ray cells" of the root, derived by septation of vertically elongated procambial cells (Fig. 4), to the normal, radially elongated cells of the secondary body, the individual ray initials undergo extensive changes in cell shape. This often leads to the formation of long projections extended in radial or vertical planes. These irregular cells are most abundantly developed in the roots of the Pinaceae, and are most frequent in *Cedrus*. Figure 4 shows a radial longitudinal section of the root of *Cedrus libanitica* Trew. The completely independent, almost amoeboid development of the newly formed ray cells is readily apparent. Transition to the radially elongated shape is delayed, so that long vertical prolongations of the cells are retained. In figures 3 and 6 these are most frequent between the corners of neighboring tracheids. This relation to the tracheids, seen in transverse sections, suggests a discontinuous system of intertracheary wood parenchyma. The transition to more normal ray structure is illustrated in figure 12.

In connection with ray ontogeny in coniferous roots, it is interesting to note the ray structure of the Carboniferous genus *Sphenophyllum*. Scott (1920) considered the secondary xylem of certain species of *Sphenophyllum* to have a unique system of intertracheary wood parenchyma. In transverse sections of favorably preserved specimens parenchymatous elements are interspersed between the rounded corners of adjacent tracheids in an apparently discontinuous manner (Fig. 2). However, in radial longitudinal sections, these parenchymatous cells possess radially oriented projections which connect the individual cells in the semblance of wood rays. If we compare with *Cedrus* roots, it seems clear that this anomalous parenchyma is the result of a delayed transition from primary to secondary ray tissue. Owing to the modified ray ontogeny in the secondary body of *Sphenophyllum*, the appearance of an intertracheary system of wood parenchyma is more pronounced than in coniferous roots, but the difference is purely quantitative. I have seen similar structure in the roots of *Medullosa* and of *Cordaites*.

Ray Origins in the Secondary Body

The cambium of the conifers or of the dicotyledons is composed of two distinct types of cells, the large, vertically elongated or fusiform initial, and the much smaller, nearly isodiametric ray initial. The fusiform initials of the conifers give rise to the tracheids and wood parenchyma of the xylem, and to the sieve tubes, parenchyma and fibers of the phloem. The ray initials form the ray tissue of both xylem and phloem. With the rapid increase in girth that results from secondary growth, the vascular rays that originated in the primary body become more and more widely separated. New rays of secondary origin are formed by the lateral meristem as the primary rays diverge. These originate in the cambium by cellular changes in the fusiform initials. The nature of these changes is quite complex, and difficult to ascertain. It seems clear that there are four quite distinct types of ray origins in the secondary body, which, taken collectively, account for all the varied ray structures found in the Coniferae. These are as follows:

(1) a single ray initial formed at the end of a fusiform initial;
(2) a single ray initial formed at the side of a fusiform initial;
(3) a vertical series of individual ray initials derived by segmentation of a fusiform initial;
(4) one or more vertically adjacent single-celled rays formed by xylem divisions of those initials which on the phloem side give rise to the so-called radial plates.

From this it follows that most ray origins in the secondary body are single cells. Indeed, it is quite rare in the older (i.e., later-formed) wood of conifers to find ray origins of more than one initial. On the other hand,

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Explanation of Figures 1–6

Fig. 1. *Keteleeria Davidiana* (Bertr.) Beissn. Transverse section of stem showing relation of primary ray origins to the fascicular and interfascicular segments of the primary body. ×50.

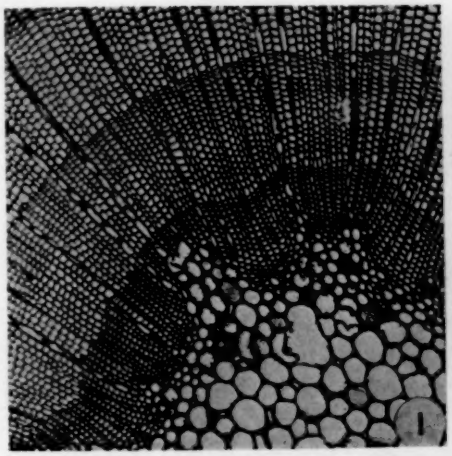
Fig. 2. *Sphenophyllum plurifoliatum* Will. and Scott. Transverse section. Cellulose nitrate peel, Iowa coal ball. Note the apparent discontinuity of rays similar to that illustrated in figure 6. ×13.

Fig. 3. *Cedrus libanitica* Trew. Transverse section of a root showing apparent discontinuity of rays in early formed secondary xylem. A transverse view of the structure shown in figure 4. ×100.

Fig. 4. *Cedrus libanitica*. Radial longitudinal section of root showing ray origin from "primary ray cells" of the root. Note the extremely irregular shape of ray cells, with their radial and vertical prolongations. ×100.

Fig. 5. *Cupressus macrocarpa* Gordon. Radial longitudinal section of root showing the origin of two new rays and the increase in height of the rays by transverse anticlinal divisions. ×100.

Fig. 6. *Cedrus libanitica*. Transverse section of a root showing apparent discontinuity of rays in early formed secondary xylem. ×35.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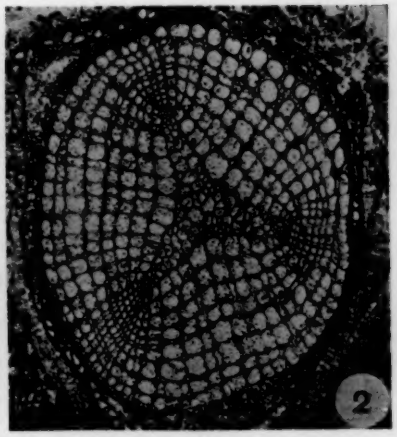
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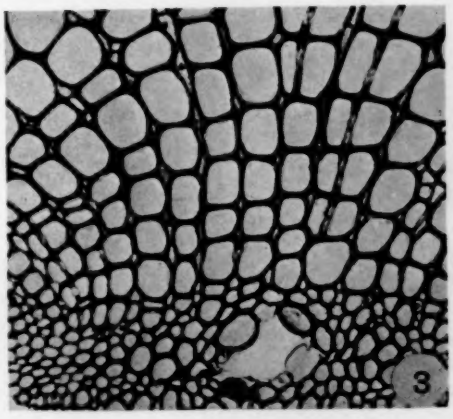
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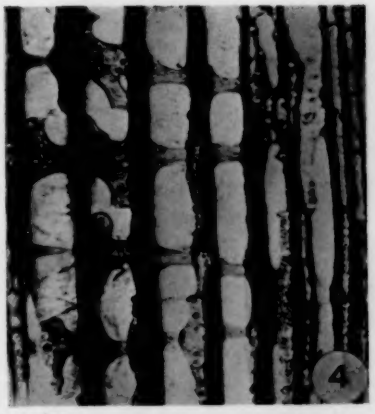
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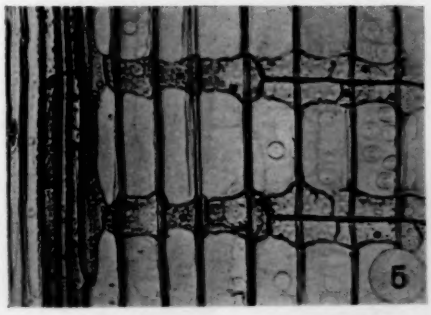
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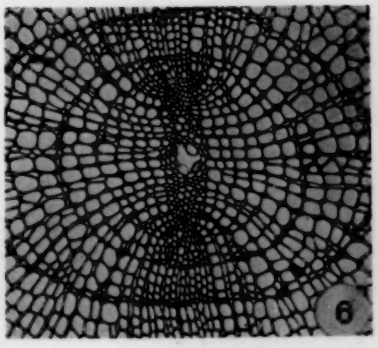
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in the earlier-formed portions of the secondary body, particularly in the root, the segmentation of an entire fusiform initial may give rise to a vertical series of ray initials. From this vertical series several rays of two or more cells can be formed very near the place of origin by the vertical approximation of the component initials. Usually, however, when segmentation occurs, the individual ray initials continue radial elongation and periclinal divisions independently of the surrounding tissue. Subsequent transverse anticlinal divisions of the initials may bring two or more low rays which are increasing in height into vertical proximity, which results in the formation of a high uniseriate ray. The processes involved in the increase and decrease in height of rays will be dealt with later.

The four methods of origin of ray initials in the secondary body differ somewhat in cytological details. Each type will be discussed separately.

(1) Ray origin by division at the upper or lower end of a fusiform initial is the predominating method in all conifers. It is this type that both Schmidt and Klinken described as the apparent means of formation of new ray tissue in the cambium of conifers. Inasmuch as they were concerned only with older stem tissues it is not surprising that their conclusions accord with other evidence. Any truly radial section of coniferous wood reveals this process. The details of the cellular changes involved are frequently obscured by the apical growth changes which occur in the xylem during differentiation. Because of this difficulty Schmidt and Klinken failed to offer proof of their conclusions.

In this study definite evidence was obtained that cell divisions actually occur at or near the apex of cambial fusiform initials in the formation of new ray initials. The use of serial tangential sections of the phloem avoided the confusing changes that characterize differentiation in the xylem. One-celled rays were traced outward in successively older regions of the phloem until their exact means of origin was determined. In most of the sequences that could be completely traced, the divisions occurred at or near the tips of fusiform initials.

In the cambium illustrated in figure 7 the division that gave rise to a new ray initial occurred shortly after an anticlinal division of the fusiform initial. Such cell divisions in the ends of fusiform initials may involve the entire apex of the initial, in which case the cell is truncated and thereby decreased in length, or they may occur at varying distances from the end. The two positions of newly-formed walls are shown in figure 17. In 17*b* the cambial initial is not decreased in length since the cell plate twice intersects the same side-wall of the parent cell, whereas in 17*a*, the entire end of the fusiform initial is involved in ray initial formation, so that the initial is decreased in length by the height of the ray initial formed. These types of

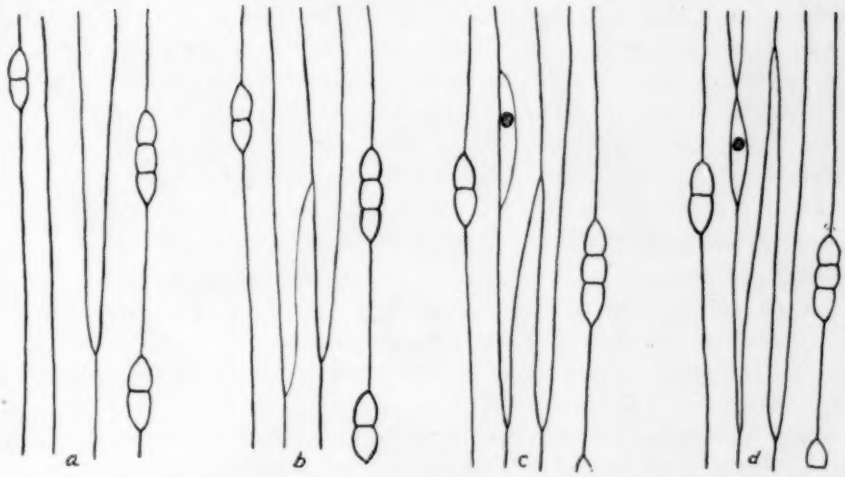

Fig. 7. *Cedrus libanitica.* Serial tangential sections of phloem, showing the origin of ray initials in the cambium; in *a* the condition in the cambium before anticlinal division of fusiform initial; in *b* anticlinal division of fusiform initial; in *c* the origin of a ray initial at the side of a fusiform initial. *d* illustrates further change in size and shape of ray and fusiform initials during successive divisons in the cambium. ×180.

end-wall formation are due to varying orientation of the phragmoplasts during cytokinesis.

The validity of this relation between the position of the cell plate and the size of the fusiform initial is borne out by a careful study of radial sections of the xylem. Figures 14 and 15 illustrate ray origins from the ends of fusiform initials. In figure 14 the formation of a ray cell did not decrease the length of the parent initial, as is indicated by the increasing length of successive cells in the row of tracheids. In figure 15, on the other hand, there is a reduction in length of the tracheary daughter cells equivalent to the height of the newly-formed ray cell.

The origin of ray initials at the ends of fusiform initials is therefore of two types: (a) the cell plate twice intersects the same side-wall of the parent fusiform initial; (b) the cell plate cuts off the end of the fusiform initial.

The cytology of such a series of cellular changes presents certain interesting problems; for example, that of the behavior of the nucleus. The nucleus ordinarily is central in the cell during the frequent periclinal divisions by which increase in thickness of xylem and phloem is accomplished. However, it is clear that when anticlinal or pseudotransverse divisions occur in cells of the size and shape of fusiform initials very extensive nuclear migrations must occur after formation of the cell plate. The two nuclei that result from the division migrate to the central regions of the

daughter cells before further periclinal divisions occur. Moreover, if the ray initial originates as is indicated in the series of diagrams in figure 7, still further nuclear movements take place. In this case the daughter nucleus of the upper, newly-formed fusiform initial migrated from its recently assumed central position, divided near the end of the cell and returned to the center before the succeeding periclinal division.

In the formation of a ray initial in this manner there is a complex series of nuclear movements indicated by the following sequence:

(a) an original central position of the nucleus in a free fusiform initial;
(b) an anticlinal cell division, followed by migration of the daughter nuclei to the centers of the resulting cells;
(c) a periclinal division of the two fusiform initials, with both nuclei remaining in a central position;
(d) a migration of the nucleus of one fusiform initial to the apical region;
(e) the formation by cell division of a ray initial near the region of the preceding anticlinal division;
(f) a remigration of the nucleus of the fusiform initial to the center of the cell;
(g) the normal periclinal division of both ray and fusiform initials.

The actual time involved in these nuclear migrations is apparently very brief. In hundreds of sections of white pine cambium, killed and fixed at the time of greatest rapidity of cell division, no division figures were seen in the ends of fusiform initials. However, several nuclei were observed in the apices of initials. Figure 13 shows the nucleus of a fusiform initial of *Pinus Strobus* L. near the extreme end of the cell. It is evident that remigration of the nucleus occurs very quickly after the formation of the ray initial. This inference is substantiated by the fact that the nucleus is in the center of the cell during each periclinal division of the initial.

(2) Origin from the side of fusiform initials is another frequent source of ray initials in coniferous cambia. The cell division that gives rise to such

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Explanation of Figures 8–12

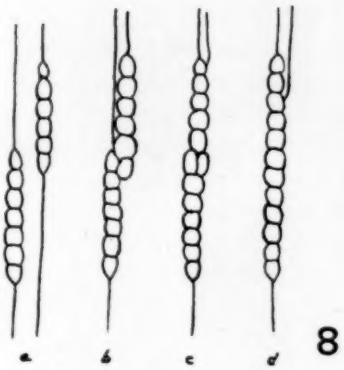
Fig. 8. *Taxus baccata* L.. Fusion of two rays by the loss of an intervening fusiform initial. Redrawn from Klinken.

Fig. 9. *Taxus baccata.* Splitting of ray by apical growth of fusiform initial. Redrawn from Klinken.

Fig. 10. Diagram of the relative size and shape of erect cell initials and ray initials in *Pinus Strobus; a,* the tangential, and *b,* the radial aspect.

Fig. 11. *Pinus resinosa* Aiton. Radial longitudinal section of xylem showing the origin of the ray from a cambial initial that previously functioned in the formation of erect phloem cells. Redrawn from Chrysler. ×225.

Fig. 12. *Cedrus libanitica.* Radial longitudinal section, showing origin of a ray and transition from vertically to radially elongated ray cells. Note amoeboid appearance of ray cells. ×150.



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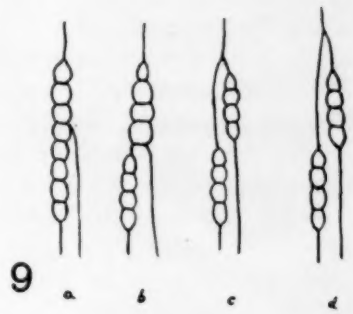

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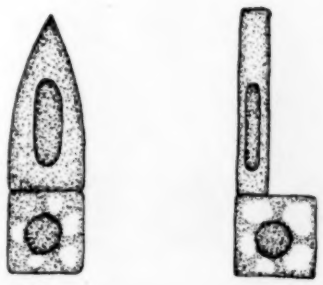

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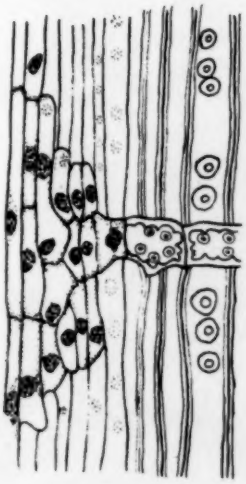

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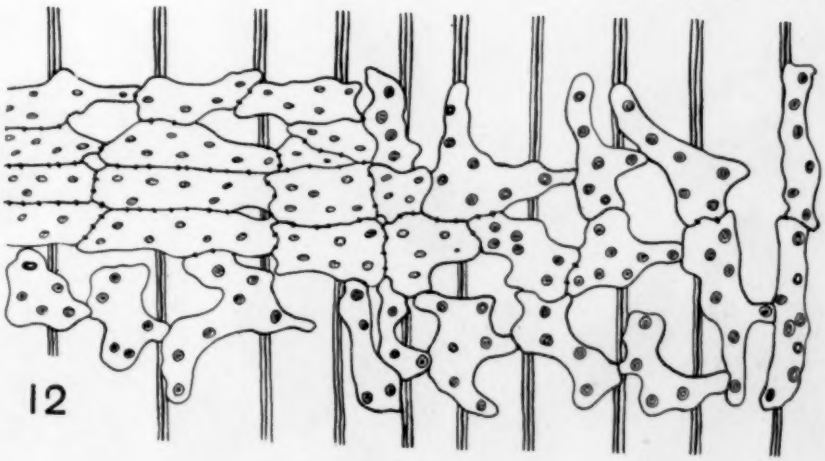

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ray initials occurs at or near the central region of the fusiform initial. From the standpoint of its cytology it is therefore merely a modification of the first type. All degrees of transition exist between these two positions of ray cell formation. Figure 21 is a photograph of the cambium of *Pinus Strobus* showing the formation of a ray initial laterally from the parent fusiform initial. The figure also illustrates the vertically elongated shape of newly-formed ray initials. This vertical elongation of the first formed derivatives of such initials (Fig. 23) makes it possible to recognize ray origins in radial longitudinal sections of the xylem. The immediately succeeding ray cell may be of a very different shape, with its long axis oriented in the radial plane, as shown in figures 14 and 23. In the Taxaceae, Cupressaceae, and Araucariaceae, the transition from the erect, newly formed ray cell to the succeeding radially elongated cell may be very

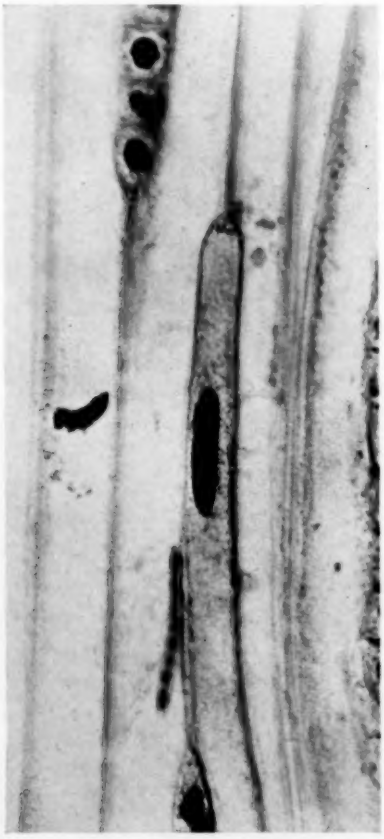


Fig. 13. *Pinus Strobus* L. Tangential longitudinal section of cambium, showing position of nucleus in apex of fusiform initial. ×280.

abrupt, with complete contiguity between the two cells, as is shown in figure 15. In the Pinaceae and many of the Taxodiaceae, on the other hand, the newly formed cells are frequently isolated, and considerable time may elapse during successive divisions before a radial continuity of the cells is brought about. Compare figures 23 and 24.

(3) The two methods of ray origin discussed above account for the formation of most new rays in the older (later-formed) secondary xylem of coniferous stems and roots. As the growth rate slows with increasing age, there is a tendency towards the restriction of ray origins to single cells derived from the ends or sides of fusiform initials. However, in young, rapidly growing stems, and more particularly in roots, there is a somewhat different mechanism involved in the formation of ray tissue, the segmentation of fusiform initials. This term as used here connotes a series of transverse divisions in a fusiform initial which result in the formation of a vertical series of cells. Whether an entire fusiform initial is converted into ray initials is extremely difficult to ascertain, since the portion of the fusiform initial which may fail to form ray initials is lost from the cambium. In most of the sections that afforded critical evidence it was found that the number of individual rays that originated by the segmentation of a fusiform initial was always less than would be expected from a cell of such dimensions. In other words, in this process of septation a portion of the segmented initial fails to divide periclinally. This portion is either differentiated as a xylem element or is pushed out of the cambium by the surrounding fusiform initials.

In the early-formed secondary xylem of coniferous roots, however, the segmentation of an entire fusiform initial into ray initials is not infrequent. Such complete transformations are rare or absent in corresponding regions of the stem. It is chiefly this difference in cambial behavior which maintains the greater abundance of ray tissue in the root than in the stem.

In general, segmentation of a cambial initial gives rise to a series of one-celled rays at varying distances from one another. The separation of these originally contiguous cells is brought about in the same manner as the transition from primary to secondary ray tissue. There is a shift in the orientation of the long axis of the cell, and almost invariably a tendency for each cell to separate from those above and below. Vertical fusion of these separate one-celled rays may occur subsequently, but it should be emphasized that high, many-celled rays in the conifers do not originate as such in the cambium but always result from a series of ontogenetic changes.

Segmentation of fusiform initials to form ray initials is not restricted to the younger portions of either root or stem, but may occur, though much less frequently, in the older wood. This is particularly true in those species which normally have diffuse wood parenchyma.

(4) The fourth means of origin of ray tissue is the derivation of ray initials from radial plates. The term radial plate has been used by Chrysler (1913) to designate certain radially arranged sheets of parenchymatous tissue characteristic of the phloem of Pinaceae. The significance and distribution of radial plates are a problem separate from that dealt with in this study, although certain histological details of the plates will be discussed in more detail later. The cambial initials that give rise to the plates are derived from fusiform initials by the same cytological processes involved in the origin of ray initials. These radial plate initials differ from the ordinary ray initials in that they remain erect, and give off chiefly phloem derivatives. In general, the radial plate initials are quickly lost from the cambium if they are not in close proximity to the marginal initials of preexisting rays. With increase in extent of the phloem, therefore, the plates frequently become recognizable as distinct sheets of parenchymatous cells, often completely dissociated from the phloem rays. However, the radial plate initials that border upon or are in proximity with the marginal initials of a ray continue meristematic activity indefinitely, giving rise to a border of erect cells along the margin of the ray. Chrysler (1913) first pointed this out and concluded that it was due to the localized activity of the initials that give rise to a radial group which was in vertical contact with a ray. Chrysler showed further that in radial plate initials dissociated from rays cambial activity may be localized in the median region of the group with the resulting origin of one or more one-celled rays in the xylem. This process takes place by xylem-forming divisions of the radial plate initials in the cambium.

It is of interest to note that this origin of ray tissue cannot be explained by a study of serial tangential or of radial sections of the xylem only. The ray initial, when it first gives rise to a xylem derivative, has already functioned for a varying length of time as an erect cell initial of a radial plate (Fig. 11); hence its first xylem derivative has not the same spatial or cellular relation to the surrounding tracheary elements as the original ray initial had when it was formed in the cambium.

In general there is a strong tendency throughout the Coniferae to restrict the formation of new ray tissue to a single-celled origin in the cambium. These newly formed single ray initials are elongated to varying degrees in the vertical plane. Their shape and orientation are usually in striking contrast to those of the subsequently formed radially elongated or procumbent ray cells. The ray initials originate by divisions in the fusiform initials, never from differentiating tracheids as implied by Thompson, nor from the ends of sieve tubes as noted by Chrysler (1913). Frequently the first xylem derivatives of newly formed ray initials are tracheary rather than parenchymatous (Thompson, 1910; Bannan, 1934). The relative

frequency of the two types is variable, however, so that no great importance can be attached to the occasional occurrence of ray tracheids at or near the point of origin of the ray.

Ray Ontogeny in the Secondary Body

Klinken analyzed in detail the development of the xylem rays in the secondary wood of *Taxus baccata*. His results apply, with minor differences in detail, to all groups of the conifers, particularly to those in which the radial plates are absent or poorly developed. By means of serial tangential sections, Klinken found that individual rays during their development tend to acquire a fairly constant height, in terms of cell number. That is, low rays increase in height, while high rays decrease in height. The two processes operate independently. The present study corroborates Klinken's results, although the presence of radial plates greatly complicates the ontogenetic stages in the Pinaceae and to a lesser degree in the Cupressaceae and Taxodiaceae. Since the two processes involved in ray ontogeny are antithetic they will be considered separately.

(1) *Increase in Height of Rays.*—Increase in height of rays is effected most frequently by simple transverse anticlinal division of the ray initial in the cambium. In this way two ray initials are formed from one. In isolated ray initials this frequently occurs shortly after their formation in the cambium, as shown by figures 5 and 14. In rays that have already attained a height of four or more cells, the transverse anticlinal divisions are restricted to the margins of the ray. In the Coniferae there are neither vertical nor transverse anticlinal divisions of the initials in the center of the ray, such as so frequently characterize ray development in the dicotyledons.[1]

Although they are frequent, the total effect of transverse anticlinal divisions of marginal ray initials is not great enough to cause the formation of the very high rays found to a varying extent in nearly all coniferous woods. This is more apparent when it is considered that the transverse anticlinal divisions are not only restricted to the marginal initials of the ray, but are less frequent as the ray increases in height. It is true that in the root wood of Pinaceae, successive transverse anticlinal divisions of the marginal ray initials may give rise to sheets of ray tissue of considerable vertical extent. However, the very high rays of both root and stem arise in the Pinaceae as in other Coniferae by an entirely different process, ray fusion.

The fusion of adjacent rays was observed by Kny and later by Klinken in his detailed study of ray development in *Taxus baccata*. Klinken found that rays separated by tracheidal elements frequently came together by

[1] Except in abnormal cases and the very old wood of *Sequoia*.

the loss from the cambium of the intervening fusiform initials (Fig. 8). He found further that if the two rays overlapped after fusion the biseriate portion of the resulting ray became uniseriate by a loss of the ray initials on one side of the biseriate portion (Fig. 8). The new ray that resulted from this lateral fusion was therefore always uniseriate and equal in height to the total vertical extent of the two pre-existing rays. Bizarre as this seems to be, the loss of fusiform initials is rather common in coniferous cambia. Its frequency is evidenced not only by observed ray fusion but also by the following considerations. The high rays not only fail to increase their height extensively by anticlinal division of the marginal initials, but instead frequently tend to decrease in height by a loss of the initials from the margins or central portions. In other words, the very high ray is only a temporary phase of the development of ray tissue. Hence the continued formation of high rays depends on a recurrent loss of fusiform initials from the cambium.

In the Pinaceae, and to a lesser extent in the Taxodiaceae and some genera of the Cupressaceae, the formation of high rays in the xylem depends on another peculiarity of development, the meristematic activity of the initials that give rise to the radial plates. Certain initials in the radial groups, chiefly those associated with the margins of the rays, may give rise to xylem derivatives which are marginal on the ray. Two rays closely approximated vertically and not separated by fusiform initials often fuse by the meristematic activity of such radial plate initials on their margins.

In general, the marginal xylem ray cells formed by radial plate initials are distinct from the other cells of the ray. Whether they are parenchymatous or tracheary, erect or radially elongated, depends on the species, but all marginal ray tracheids and marginal xylem ray parenchyma cells of coniferous woods are derived from initials which at one time were part of radial plate tissue. Since the initials that give rise to radial plates originate in the cambium by the same sequence of cytological changes which characterize the origin of ray initials, it is not surprising that transitions occur between the typically vertically elongated or erect initials which form plate cells and the characteristic nearly isodiametric initials of the ray proper. There are, however, certain other histological differences between the two types of initials, as well as their derivatives, which will be considered below.

Radial plate initials that join two vertically adjacent rays are frequently very high and commonly give rise to xylem cells of very irregular shape. The height of these cells depends on that of the initials from which they were formed, and is not, as Thompson suggested, indicative of a stage in the transition of tracheids to ray tracheids. Sometimes the erect initials that bring about a fusion of rays become continually shorter and assume

the size and shape of the ordinary initials of the two rays. This is usually accompanied by anticlinal divisions in the erect initials, and often by a change in the xylem derivatives of the latter from the tracheary to the parenchymatous type, which completes the fusion of the rays. In those Pinaceae in which ray tracheids are abundant, such as *Pinus* and *Larix*, there is seldom a change from the tracheary to the parenchymatous type. It is common, therefore, to find in these genera rays with ray tracheids not only marginal but also intervening in the central portions. Such rays commonly arise either by the lateral fusion of two rays already possessing marginal ray tracheids, or by the vertical fusion of two or more rays through the meristematic activity of erect cell initials adjacent to them in the cambium.

Vertical fusion of two very closely approximated rays may occur by two other means, both of which take place irrespective of radial plates and hence may be found in all conifers. Occasionally in radial longitudinal sections two rays that have continued independently of each other for some distance suddenly fuse by the vertical expansion of the adjacent marginal cells. Rays so fused often separate shortly, and may remain separate or fuse again.

It might be thought that this is merely the appearance in radial section of the effect of the loss of a fusiform initial that separates two rays both laterally and vertically adjacent. However, the sequence of the tracheids in the radial rows, as well as the fact that a subsequent separation may occur after fusion, indicates that this is not so. There is an actual approach and adhesion of the plastic cell walls of the ray initials in the cambium.

The last mechanism whereby vertical fusion of rays may take place is the occurrence of transverse anticlinal divisions in the marginal initials of two vertically adjacent rays. The increase in height brought about by the addition of new cells at the margins brings the two rays into contact with each other and results in the formation of a high ray.

(2) *Decrease in Height of Rays.*—Decrease in height of rays was accurately described by Klinken, who found that two mechanisms are involved. It may occur by the loss of ray initials from the cambium, or by the splitting of one high ray in the cambium into two smaller rays.

Except in genera in which extensive reduction of ray tissue is indicated by predominantly low rays, the loss of actively dividing ray initials from the cambium is comparatively rare. When it occurs, the initial may be lost either from the central region of the ray or from the margin. Figure 18 shows the loss of an initial from the central portion of a ray of *Taxus baccata*. The drawing was made from a photograph of a section that included phloem, cambium and xylem. On the extreme right is the last xylem derivative of the initial which has been "lost" from the cam-

bium, while on the left the "initial" may be seen fully differentiated into a phloem ray cell.

The decrease in height of rays by splitting depends on the rate and extent of elongation of fusiform initials in the cambium. As shown by Bailey (1923) the increase in girth of coniferous cambia is accomplished chiefly by anticlinal or pseudotransverse divisions in the fusiform initials. The two daughter initials that result from this division elongate until they are as long as the initial from which they were formed. Elongation is restricted to the cell apices, which penetrate the intercellular substance between the surrounding initials. The actual separation of the large ray into smaller units is caused by the intrusion of the apex of the fusiform initial into the intercellular substance between the ray initials (Fig. 9). The apices of the fusiform initial and of its xylem daughter cells continually elongate during successive divisions and bring about a permanent separation of the two portions of the ray. It is apparent that the split must occur in the cambium and not in the daughter cells of the xylem, since changes in the latter during differentiation would not affect cellular relations of the cambial initials.

From the mechanics of ray splitting by the apical growth of fusiform initials it follows that high rays undergo separation into smaller units more frequently and more readily than do low rays. The purely statistical chances for a cleavage in the ray increase with the height of the ray. Therefore, the reduction in ray height by this means is a chance phenomenon, which tends towards the elimination or reduction of very high rays.

These theoretical considerations are borne out by observation. In radial longitudinal sections of coniferous xylem it is chiefly the higher rays that are split; only occasionally is a four- or five-celled ray divided.

Explanation of Figures 14–18

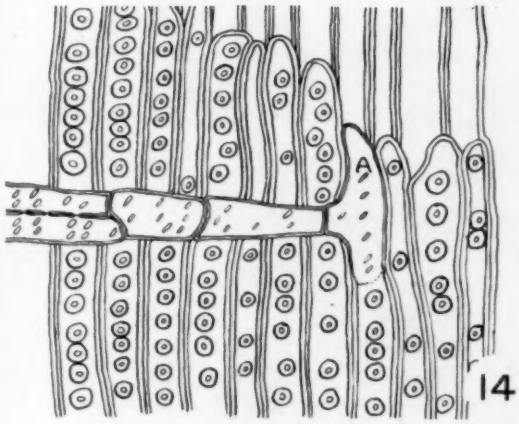
Fig. 14. *Ginkgo biloba* L.. Radial longitudinal section of stem, showing the relation of ray origin to the end of a tracheid, and indicating the origin of the ray initial from the end of a fusiform intial. Note sudden transition in shape between first-formed (A) and succeeding ray cells. ×210.

Fig. 15. *Amentotaxus argotaenia* (Hance) Pilger. Radial longitudinal section of stem, showing the origin of a ray in relation to tracheids. The ray initial was formed at the apex of the fusiform initial whose xylem derivatives are indicated (A and B). Contrast with figure 14. ×210.

Fig. 16. Diagram of the origin of erect cell initials from fusiform initials. *a*, origin at the side of initial; *b*, from the end of initial. The size of erect cell initials in proportion to fusiform initials is exaggerated.

Fig. 17. Diagram of two types of end origin of ray initials from fusiform initials. *a*, the entire end of the fusiform initial is involved in ray initial formation; *b*, only a lateral portion of the end.

Fig. 18. *Taxus baccata*. Radial longitudinal section of xylem, cambium, and phloem, showing loss of ray initial from cambium. Note the correspondence of cells on both sides of the cambium (A and A'). ×210.



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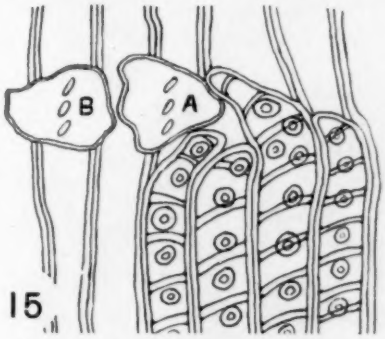

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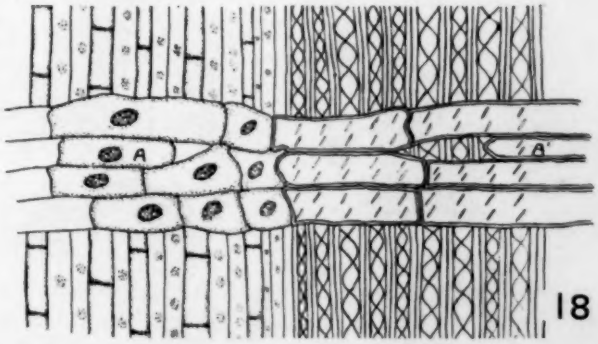

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Radial Plates and Erect Cells

It was pointed out above that the radial plates are produced by initials whose origin in the cambium follows a somewhat modified series of cytological changes similar to those involved in the formation of ordinary ray initials. Apparently the plate initials originate most frequently by a division at the side of a fusiform initial. The wall formed in this division is long and intersects at its opposite ends the same radial side wall of the fusiform initial. The large vertically elongated cell so formed gives rise to a strand of smaller upright or erect cells by a series of transverse divisions. Figure 16*a* shows the first stage in the formation of a radial plate, before the occurrence of transverse anticlinal divisions. The plate initials may also originate at the ends of fusiform initials, as is shown in figure 16*b*. Occasionally the large initial formed by the original division in the fusiform initial fails to divide transversely, so that a short fusiform initial is produced. This is much higher than the normal erect cell initials, though otherwise similar. Such short initials may give rise on the xylem side to the short tracheids occasionally found in the wood of *Pinus*, *Picea*, and *Larix*.

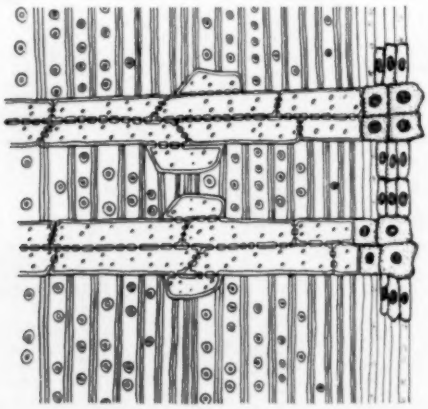


Fig. 19. *Abies balsamea* (L.) Mill. Radial longitudinal section of xylem, showing the relation of erect cell initials to marginal xylem ray cells. The xylem-forming divisions of the erect cell initials are less frequent than those of the ray initials. ×140.

After their formation, the radial plate initials divide for a short period, after which their meristematic activity dwindles. However, in radial plate initials that border on the marginal initials of a ray meristematic activity may persist, with the production of a border of erect cells on the phloem side of the ray and of marginal tracheids or parenchyma on the xylem side. The xylem-forming divisions of the erect cell initials bordering on ray initials are often less frequent than the divisions of the normal ray and

fusiform initials, and the xylem daughter cells are therefore scattered along the margins of the ray. Figure 19 shows this condition, very commonly encountered in *Abies*, *Pseudolarix*, and *Keteleeria*. The phloem erect cells, on the other hand, are in a consecutive sequence, so as to form a continuous marginal border on the ray. It has been observed frequently (Strasburger, 1891; Chrysler, 1913; Thompson, 1910; and Bannan, 1936) that erect cells of the phloem rays are usually coterminous with marginal xylem ray cells. Since the two cell types are derived from the same initial it follows that they will be coterminous unless delayed division of the initial causes a separation of its xylem and phloem derivatives. The xylem cells produced by erect cell initials are either parenchymatous or tracheary. Hence, both marginal ray parenchyma and marginal ray tracheids may occur not only in the same species but in the same individual ray. In general, in genera in which ray tracheids are abundant, the first xylem daughter cells of the radial plate or erect cell initials are tracheary. There may be a change from the tracheary to the parenchymatous cell type, though in *Pinus*, in which ray tracheids are very extensive, the erect cell initials give rise nearly exclusively to ray tracheids in the xylem. The difference between ray tracheids and marginal ray parenchyma is due entirely to the difference in secondary wall formation, since both have a similar origin in the cambium. Because of the close relationship between radial plates and marginal ray cells, the problem of ray ontogeny of conifers cannot be completely separated from the problem of the origin and nature of radial plates. Not only are the initials that give rise to the two tissues similar in origin, but there are also graded transitions between the two types of initials and their cambial derivatives. However, certain histological features of the radial plates or erect cells in the phloem necessitate a separate treatment, since they differentiate them from the remaining ray and phloem parenchyma.

It should be pointed out that the term "radial plate" therefore includes both the erect cells of a ray and the radial sheets of parenchymatous tissue in the phloem, whether or not these are associated with phloem rays.

A distinction between erect and procumbent phloem ray cells was made by Strasburger, who pointed out certain similarities between the former and sieve tubes. He observed that the cells on the margins of the rays in the phloem of various conifers are upright, completely lack starch, possess well-developed sieve areas, and tend to lose their cell contents contemporaneously with surrounding sieve tubes. Because of the absence of starch, the concomitantly greater "density" of the cytoplasm, and the presence of conspicuous protoplasmic connection with the sieve tubes, Strasburger designated these erect marginal cells *eiweisshaltige Zellen*. This term has been translated into English as "albuminous cells," which

expression is therefore synonymous with erect cells. In recent years the former has been more widely used; its uncritical acceptance has been unfortunate. "Albuminous" implies a fundamental protoplasmic difference between the erect marginal ray cells and the procumbent ray cells of the phloem, a difference not yet demonstrated by micro-chemical or optical means. There seems little justification for retaining a term of such definite and restrictive meaning when the basis for its usage has not been presented. There is considerable evidence that the absence of starch is not definitive of "albuminous cells." The inadequacy of this character has been noted by Chrysler (1913). My observations support the view that the presence or absence of starch is of no great importance in defining the morphological or physiological significance of erect phloem ray cells. Starch grains, though in somewhat smaller quantities than in the procumbent ray cells, were found in the erect cells of *Abies*, *Pseudolarix*, and *Pinus*, and would probably be found in the remaining Pinaceae if suitable material were examined.

In tangential sections of both the phloem and cambium of Pinaceae, stained in Heidenhain's haematoxylin or aniline blue, the erect cells are very frequently distinguished from the other cells of the ray by the apparent greater intensity of their staining (Figs. 20, 22). This difference has been attributed to a greater density of the protoplasm concomitant with the albuminous nature of the cells. However, an analysis of the factor that might be responsible for the apparent staining difference indicates that the cause is to be found in the physical rather than in the chemical properties of the cells. The orientation of the long axis of the erect cell is vertical rather than horizontal. This factor and the very small radial dimension of the cell make it very probable that even a thin tangential section will include entire cells, with both tangential walls and protoplasts intact. The procumbent ray cells, on the contrary, are radially elongated, and the chances are small that an intact cell will be included in sectioning. This difference of shape between erect cells and phloem ray cells is true

Explanation of Figures 20–24

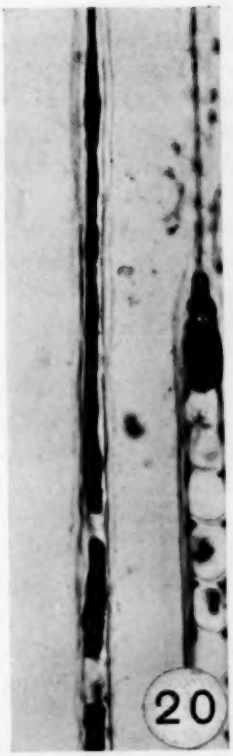
Fig. 20. *Pinus Strobus*. Tangential longitudinal section of phloem, showing darkly staining cells of radial plate tissue; stained in aniline blue. ×250.

Fig. 21. *Pinus Strobus*. Tangential longitudinal section of cambium, showing origin of ray initial by division at side of fusiform cambial initial. ×650.

Fig. 22. *Pinus Strobus*. Tangential longitudinal section of cambium, showing erect cell initial persisting at margins of two rays; stained in Heidenhain's haematoxylin. ×310.

Fig. 23. *Cephalotaxus drupacea* Sieb. et Zucc. Radial longitudinal section of xylem, showing origin of ray. Note relation of the ray origin to the ends of tracheids. ×250.

Fig. 24. *Cunninghamia lanceolata* (Lamb.) Hook. Radial longitudinal section of xylem, showing an isolated, irregularly shaped ray tracheid. ×250.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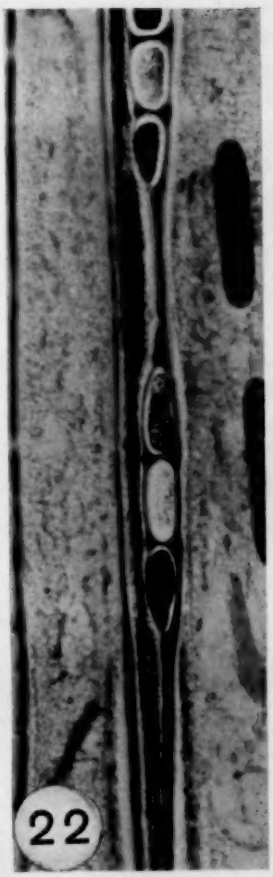
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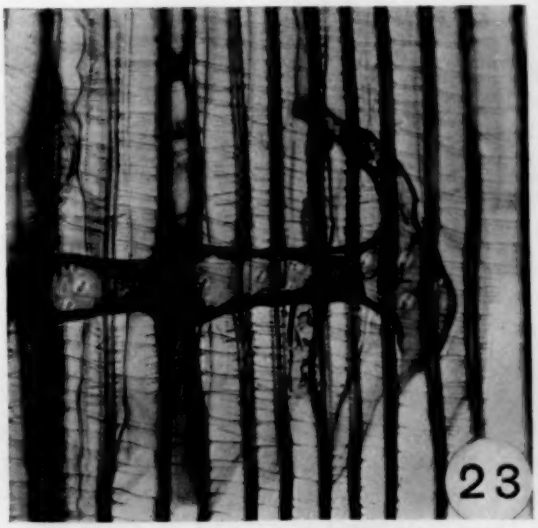
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also of their respective cambial initials. Figure 10 shows diagrammatically the comparative size and shape of erect cell initials in the cambium of *Pinus Strobus;* figure 10*a* shows the tangential aspect, figure 10*b* the radial. In the mature phloem there is a still greater difference between the two types of daughter cells in their relative radial elongation, since erect cells undergo only slight changes in cell shape during differentiation, whereas ordinary phloem ray cells tend to elongate radially.

The difference in staining of these cells in tangential section is thus due primarily to the size and shape of the cells and not to a difference in the chemical nature of their protoplasts. This conclusion is substantiated by the fact that in radial sections the two cell types show identical reactions in both color and intensity of stain.

In general, the only morphological feature of erect cells that offers any basis for the term "albuminous" is the presence of sieve areas and protoplasmic connection with the sieve tubes. The erect cells in the phloem are apparently physiologically related to the sieve tubes, since they pass through similar ontogenetic stages, and lose their contents and develop callus at the same time as the sieve tubes.

That erect cells are found to a varying extent throughout the Coniferae indicates that among living genera there is a series of evolutionary stages in the development of this tissue. In the Araucariaceae, Taxaceae, and Cephalotaxaceae, in which erect cells are absent or very scantily developed, there are no organized radial plates of tissue in the phloem, and xylem ray tracheids are nearly if not completely absent except when associated with ray origins. In the Cupressaceae and Taxodiaceae erect cells are not infrequent, and radial plate initials of brief duration in the cambium are occasionally present. However, there is no extensive development of marginal xylem ray tracheids or parenchyma. In the Pinaceae, on the other hand, the tendency to form erect cells is strong and results in the formation of extensive plates of parenchymatous tissue in the phloem (Figs. 20, 22). Correlated with the increasing tendency towards the formation of radial plates and the concomitant erect cells of the rays is the increasing frequency of ray tracheids or marginal ray parenchyma in the xylem. Ontogenetically also the erect phloem cells appear first in the development of the secondary body before any xylem derivatives are formed by the erect cell initials (if they are ever formed).

The cytological complexity of the formation of erect cells and their apparent modification of function so as to be related to sieve tubes make it appear that the development of radial plates and erect cells is a phylogenetic line of specialization which culminates in the Pinaceae, more specifically in *Pinus*. That the development of ray tracheids is entirely

dependent upon the activity of the radial plate initials is additional evidence that ray tracheids represent an anatomic specialization.

The detailed histological problems associated with the ontogeny and the phylogenetic significance of radial plates are introduced here only because they are closely related to certain aspects of ray origin and ontogeny in the Coniferae.

SUMMARY

A review of previous research on the origin and development of ray tissue in the Coniferae reveals no comprehensive treatment of the problem. Fundamental cytological details have not been closely examined.

In the first-formed secondary xylem of coniferous stems most rays extend from the interfascicular segments of the stele. In the stem the rays are very low at the beginning of secondary growth; in the root they are considerably higher. This fundamental difference in height at the origin accounts, in part, for the greater abundance of ray tissue in the root than in the stem.

A careful study of coniferous cambium and phloem shows that the ontogenetic origin of ray tissue is a highly complex process, frequently involving extensive nuclear migrations in the fusiform initials.

In the secondary body of the Coniferae the majority of new rays are formed by initials which originate at the apex or sides of fusiform initials. The ray initials originate most commonly as isolated cells not associated in vertical series. The segmentation of fusiform initials also occurs.

The cambial initials which give rise to the so-called radial plates of the phloem of certain conifers may also enter into the formation of xylem and phloem rays.

Increase in the height of rays is accomplished in the cambium by increase in cell number per ray or by the fusion of two or more rays either laterally or vertically adjacent to each other. The lateral fusion of rays involves the loss from the cambium of intervening fusiform initials.

Decrease in the height of rays takes place by the loss of ray initials from the cambium and by the splitting of high rays into smaller units. Ray splitting occurs by the elongation of fusiform initials in the cambium.

Increase and decrease of ray height occur completely independently of each other, not only in adjacent rays but in the same ray.

The cambial initials that give rise to the radial plates of certain conifers originate by the same cytological mechanism as the ray initials. The morphological significance of radial plates is not considered, but their relation to ray ontogeny is briefly described.

It is recommended that the term "albuminous cell" be dropped, because of the lack of evidence to substantiate the meaning of the term.

The writer wishes to express his sincere appreciation to Professor I. W. Bailey for his active interest and aid in this work; and to Professor R. H. Wetmore for his advice and suggestions.

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